

Terrestrial Wildlife Responses to Climate Change



Steve Beissinger

Dept. of Environmental Science, Policy &
Management, and Museum of Vertebrate
Zoology, U. C. Berkeley

Biological Impacts of Climate Change

Parmesan, C. Annual Review of Ecology, Evolution, and Systematics
37: 637-669

- 1. Phenology** - Advance of spring events (bud burst, flowering, breaking hibernation, migrating, breeding).
- 2. Mismatched Timing** - Variation in phenological response has resulted in increasing asynchrony in predator-prey and insect-plant systems.
- 3. Poleward Range Shifts** - have been documented for individual species, as have expansions of warm-adapted communities.
- 4. Disease Expansion** - Shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics.

The Ultimate Biological Impact of Climate Change: Extinction

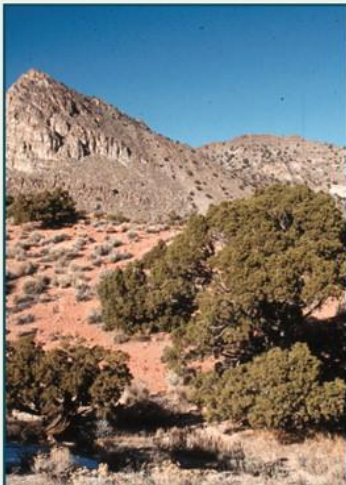
Parmesan, C. Annual Review of Ecology, Evolution, and Systematics 37: 637-669

5. Extinction - Range-restricted species, particularly polar and mountaintop species, show *more-severe range contractions* than other groups and *whole species have gone extinct* due to recent climate change.

PROBLEM – this conclusion is poorly supported. Need better historical data, which can come from collections, field notes, surveys, atlases, and species accounts.

Range Responses to Environmental Change

Toleration



Juniperus osteosperma

Habitat shift



Pinus flexilis

Migration



Picea glauca

Extinction



Picea martinezii



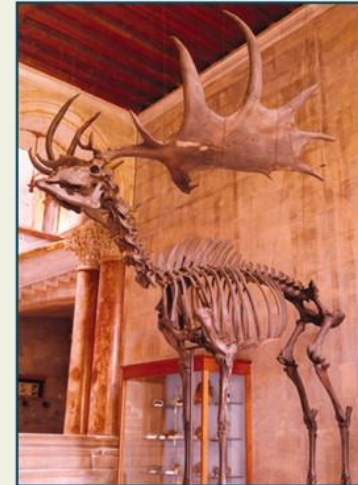
Alces alces



Cervus elaphus



Rangifer tarandus



Megaloceros giganteus

Challenges in Comparing Historical and Contemporary Data

1. *Data quality* - non-standardized survey protocols and uncertain historical locations
2. *Survey data is often limited to detection and nondetection*
3. *Ascribing causation to changes that are observed* – historical vegetation and climate data are often lacking.

The Grinnell Resurvey Project: Impact of a Century of Climate Change on Small Mammal and Bird Communities in California

2006



1930



Steve Beissinger

Dept. of Environmental
Science, Policy &
Management, and
Museum of Vertebrate
Zoology, U. C. Berkeley

Grinnell Resurvey Team

Craig Moritz



Jim Patton



Chris Conroy



Steve Beissinger



Morgan Tingley



Michelle Koo



Adam Smith

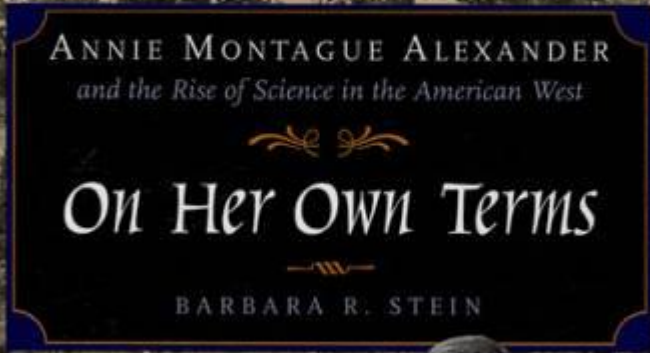


Pete Epanchin



Annie Alexander

Museum of Vertebrate Zoology was Founded in 1908



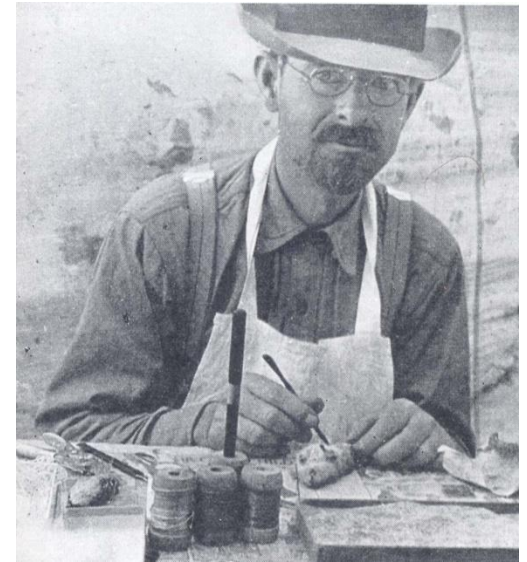
Stein 2001



Joseph Grinnell

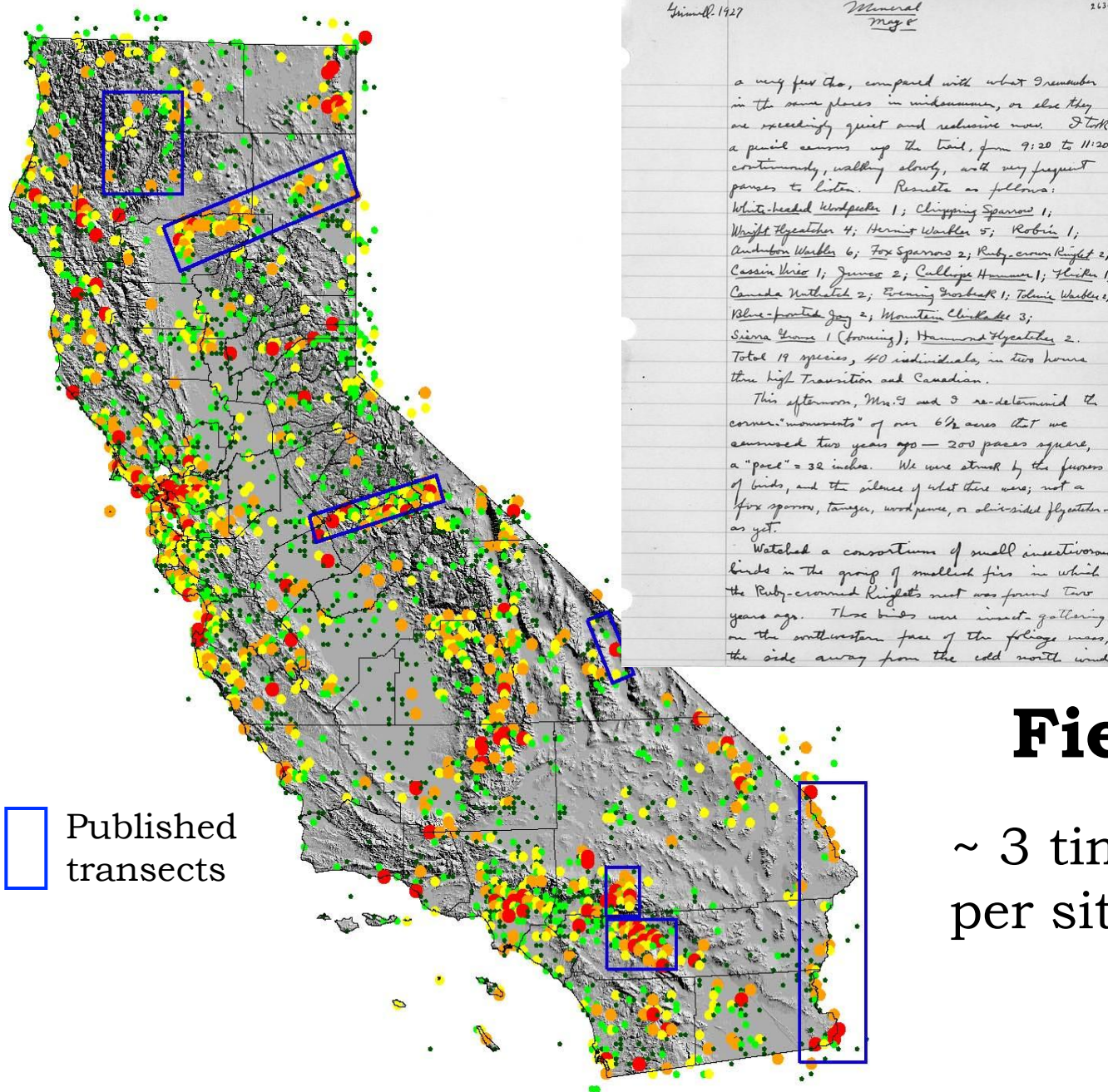
The Grinnell Legacy

“At this point I wish to emphasize what I believe will ultimately prove to be the greatest purpose of our museum. This value will not, however, be realized until the lapse of many years, ***possibly a century***, assuming that our material is safely preserved. *And this is that the student of the future will have access to the original record of faunal conditions in California and the west, where ever we now work*” (Grinnell, 1910)



**Joe Grinnell, MVZ
Director 1908-39**

Pre-1940 MVZ Specimen Locality Records



Simmons 1927

Monterey

2136

a very few tho, compared with what I remember in the same places in midsummer, or else they are exceedingly quiet and reticent now. I took a pencil census up the trail, from 9:20 to 11:20, continuously, walking slowly, with very frequent pauses to listen. Results as follows:
 White-headed Woodpecker 1; Chipping Sparrow 1;
 Whistling Flycatcher 4; Hermit Warbler 5; Robin 1;
 Audubon Warbler 6; Fox Sparrows 2; Ruby-crowned Kinglet 2;
 Cassin Vireo 1; Junco 2; Calliope Hummer 1; Flicker 1;
 Canada Nuthatch 2; Evening Grosbeak 1; Toluia Warbler;
 Blue-fronted Jay 2; Mountain Chickadee 3;
 Sierra Wren 1 (forming); Hammond Flycatcher 2.
 Total 19 species, 40 individuals, in two hours
 thru high Transition and Canadian.

This afternoon, Mrs. S and I re-determined the corner "monuments" of our 6 1/2 acres that we censused two years ago — 200 paces square, a "pace" = 32 inches. We were struck by the furrows of birds, and the silence of what there was; not a fox sparrow, tanager, woodpecker, or olive-sided flycatcher as yet.

Watched a consortium of small insectivorous birds in the group of smallish firs in which the Ruby-crowned Kinglet's nest was found two years ago. These birds were insect-gathering on the southwestern face of the foliage mass, the side away from the cold north wind.

MUSEUM OF VERTEBRATE ZOOLOGY

CENSUS SHEET

Locality: <u>Laurel Park</u>	Nature of route (zone, fauna, associations)				
Date: <u>July 26, 1928</u>	1300 to 8200 feet				
Observer: <u>J. Simmons</u>	8200 to 8750 feet				
Time in field: <u>7:20 to 12:10</u>	8750 to 9500 feet				
Approximate no. miles: <u>6 (by trail)</u>	9500 to 10,000 feet				
Species	Hours	7:20 - 8:20	8:20 - 9:20	9:20 - 10:20	10:20 - 12:10
Spotted Sandpiper	2				
Western Wood Pewee	4	3			
White-crowned Sparrow	3				
Western Robin	3	2			
Lincoln Sparrow	2				
Cassin Purple Finch	16	1			
Canada Nuthatch	3	1			
Audubon Warbler	3	6			
Sagehen Junco	17	13			
Mountain Chickadee	7				
Pacific Chipping Sparrow	5				
Ruby-crowned Kinglet	2				
Pine Siskin	2				
Golden-crowned Kinglet	7+				
Townsend Solitaire	1				
Clark Nutcracker	2	11			
Antelope Three-toed Woodpecker	1				
Hairy Woodpecker	1				
Western Tanager		1			
Savannah Hawk			1	1	
Rock Wren					2

TOTALS (hourly and grand)

Field Notes

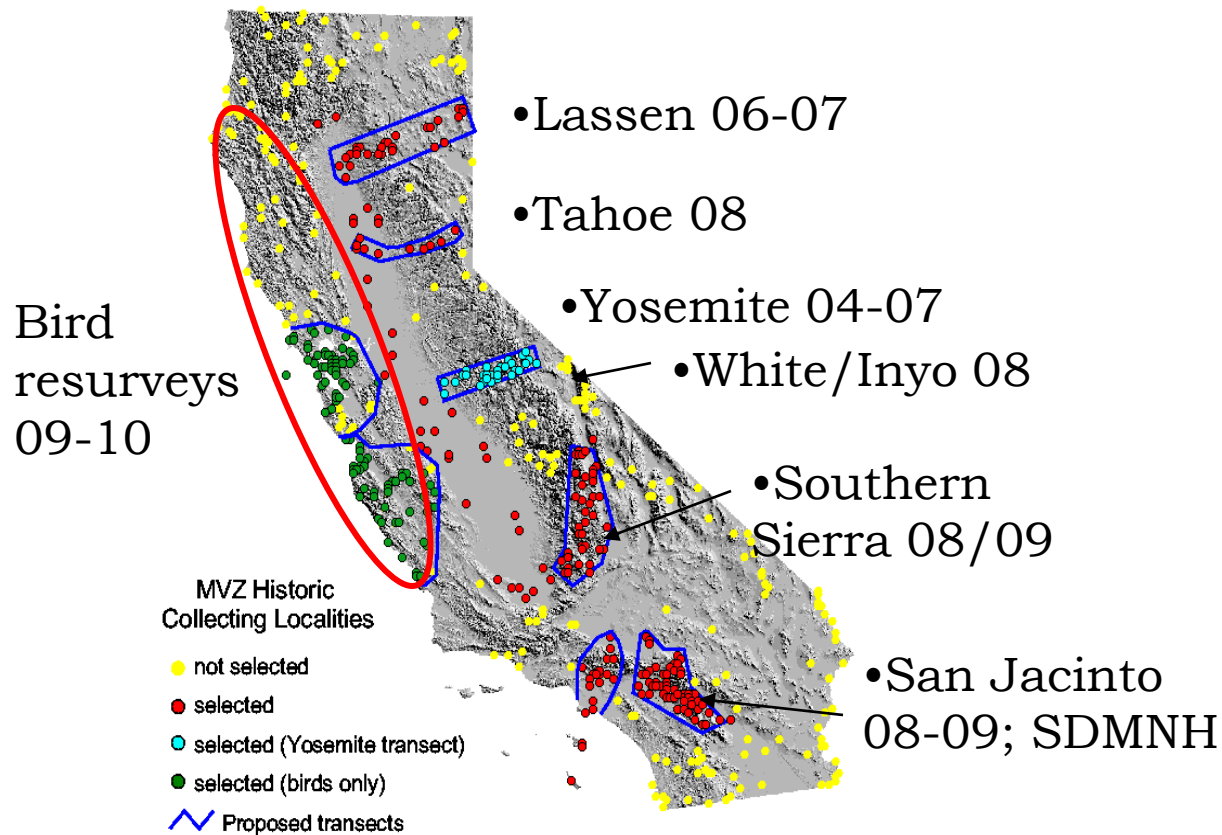
~ 3 times more species per site **observed** than **collected**

Narrative of Ward Russell, the MVZ's preparator for 40 years, doing field work with Grinnell

*(From an interview with Ward at his home in Berkeley, 4 March 1992,
by Oliver P. Pearson, Professor Emeritus and former MVZ Director)*



Grinnell Project: Status and Future

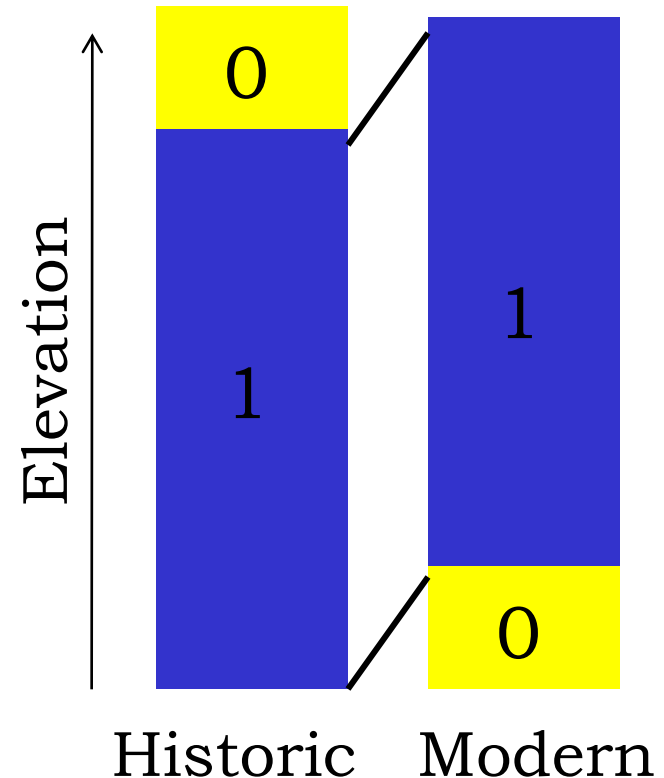


- Continuing resurveys
- Modeling past change (08-11)
- Predicting future change (09-12)

Issues in Detecting Range Change Using Historical Data

The challenge is making unbiased comparisons between historic and contemporary data:

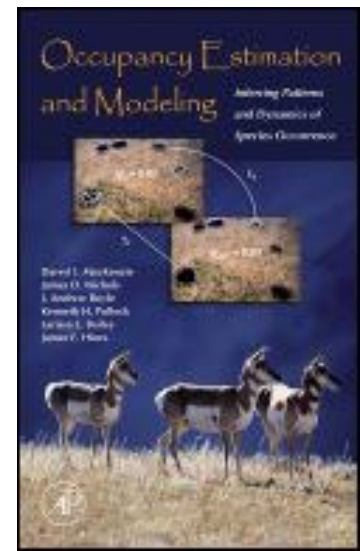
- Survey observers, methods, and effort differ over time
- Uncertainty about a “true” absence



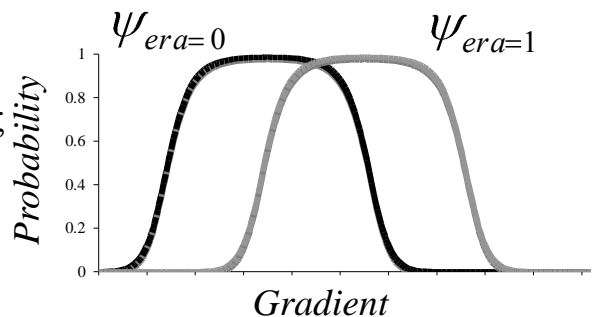
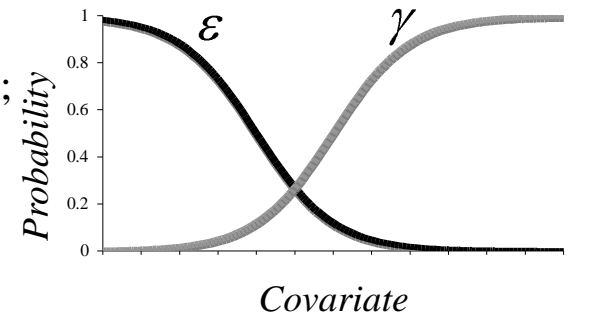
Occupancy Models

- Investigate patterns in occupancy using **presence-absence data**.
- Recognize that an observed 'absence' may be the result of a **true absence or a nondetection**.
- Depend on **repeated surveys over a short (closed) time period** to determine presence or absence of a target species.

MacKenzie et al. (Ecology 2002, 2004; book in 2006) provide a general treatment of the topic.



Parameterizations of Occupancy Models For Inferring Range Shifts

<u>Model</u>	<u>Sites</u>	<u>Modeled Parameters</u>	<u>Example Equations</u>	<u>Range Change Inference</u>
Single Season	Unpaired	ψ, p	$\text{logit}(\psi) = \beta_0 + \beta_1 \cdot \text{era} + \beta_2 \cdot \text{gradient} + \beta_3 \cdot \text{gradient}^2;$ $\text{logit}(p) = \beta_4$	
Multi-Season	Paired	$\psi_0, \varepsilon, \gamma, p$	$\text{logit}(\psi_0) = \beta_0 + \beta_1 \cdot \text{covariate} + \beta_2 \cdot \text{gradient}^2;$ $\text{logit}(\varepsilon) = \beta_3 + \beta_4 \cdot \text{covariate};$ $\text{logit}(\gamma) = \beta_5 + \beta_6 \cdot \text{covariate};$ $\text{logit}(p) = \beta_7$	

Single Season Occupancy Models

For a series of species' presences (1) and absences (0) observed in repeated surveys at each site: h_1, h_2, \dots, h_s (1,0,1,0,0,0)

$$L(\psi, p | h_1, h_2, \dots, h_s) = \left[\psi^{n_{\cdot}} \prod_{t=1}^T p_t^{n_t} (1 - p_t)^{n_{\cdot} - n_t} \right] \times \left[\psi \prod_{t=1}^T (1 - p_t) + (1 - \psi) \right]^{N - n_{\cdot}}$$

where:

ψ - the probability a species is present (occupancy)

p - the probability of detection

N - the total number of sites surveyed

T - the number of distinct sampling occasions

n_{\cdot} - the total number of sites at which the species was detected at least once

n_t - the number of sites where the species was detected at time t .

Inference from Occupancy Models About False Absence Across a Set of Sites

The probability of detection at a site (P^*), based on the number of samples at a site (k) and any covariates (e.g., trapping effort, observer), is:

$$P^* = 1 - \prod_{i=1}^k (1 - p_i)$$

The probability of a false absence from a site ($P_{fa(site)}$) is:

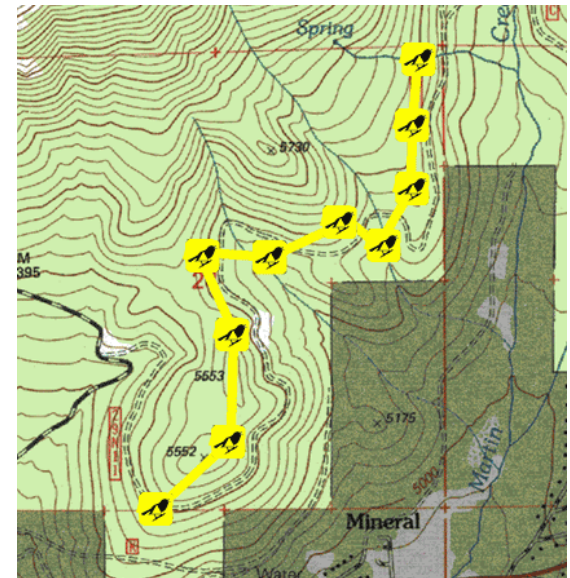
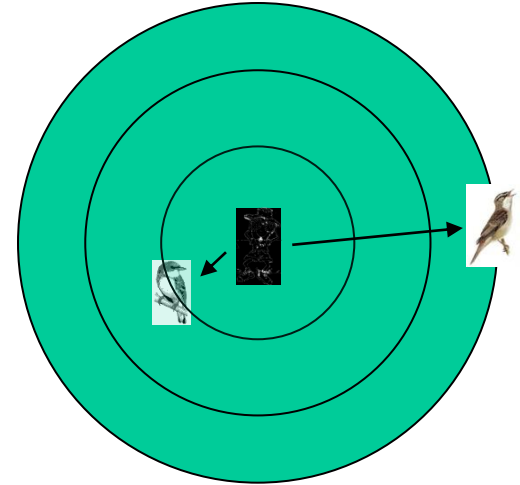
$$P_{fa(site)} = 1 - P^*_{(site)}$$

The probability of a false absence across a set of n sites (P_{fa}) is:

$$P_{fa} = \prod_{i=1}^n P_{fa(site)}$$

Challenge with Historic Bird Data: Survey Methods Change Over Time

Locality <i>To Laramie Peak</i>	Nature of route (zone, fauna, associations)					
Date <i>July 26, 1928</i>	<i>7300 to 8200 feet</i>					
Observer <i>J. Grinnell</i>	<i>8200 to 8750 feet</i>					
Time in field <i>7:20 to 12:10</i>	<i>8750 to 9500 feet</i>					
Approximate no. miles <i>6 (by trail)</i>	<i>9500 to 10,000 feet</i>					
Species	Hours	7:20 -	8:20 -	9:20 -	10:20 -	11:20 - 12:10 Totals
<i>Spotted Sandpiper</i>		2				
<i>Western Wood Pewee</i>		4	3			
<i>White-crowned Sparrow</i>		3				
<i>Western Robin</i>		3	2			
<i>Lincoln Sparrow</i>		2				
<i>Cassin Purple Finch</i>		16	1			
<i>Canada Nuthatch</i>		3	1			
<i>Audubon Warbler</i>		3	6			
<i>Sierra Junco</i>		17	13			
<i>Mountain Chickadee</i>		7				
<i>Pacific Chipping Sparrow</i>		5				
<i>Ruby-crowned Kinglet</i>		2				
<i>Pine Siskin</i>		2				
<i>Golden-crowned Kinglet</i>		7+				
<i>Townsend Solitaire</i>		1				
<i>Clark Nutcracker</i>		2	11			
<i>Antelope Three-toed Woodpecker</i>		1				
<i>Hairy Woodpecker</i>		1				
<i>Western Tanager</i>			1			
<i>Savannah Hawk</i>				1	1	
<i>Rock Wren</i>						2
TOTALS (hourly and grand)						



Timed surveys along elevational path

7 min unlimited-radius point counts along same path

Detectability Results for 43 Bird Species

Candidate Detection Models

(.)

Era

Julian day

Observer

Era + Julian Day

Era * Julian Day

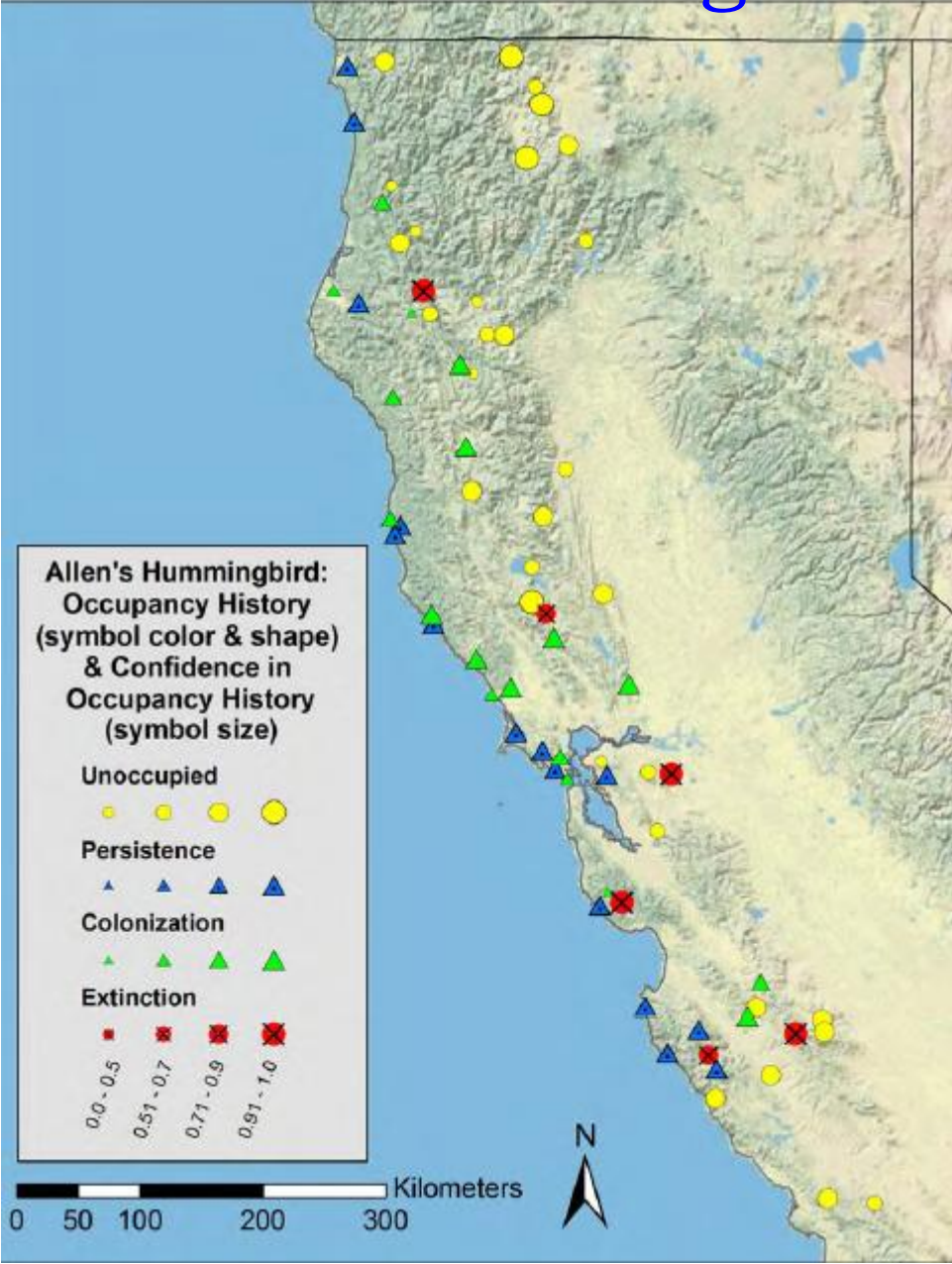
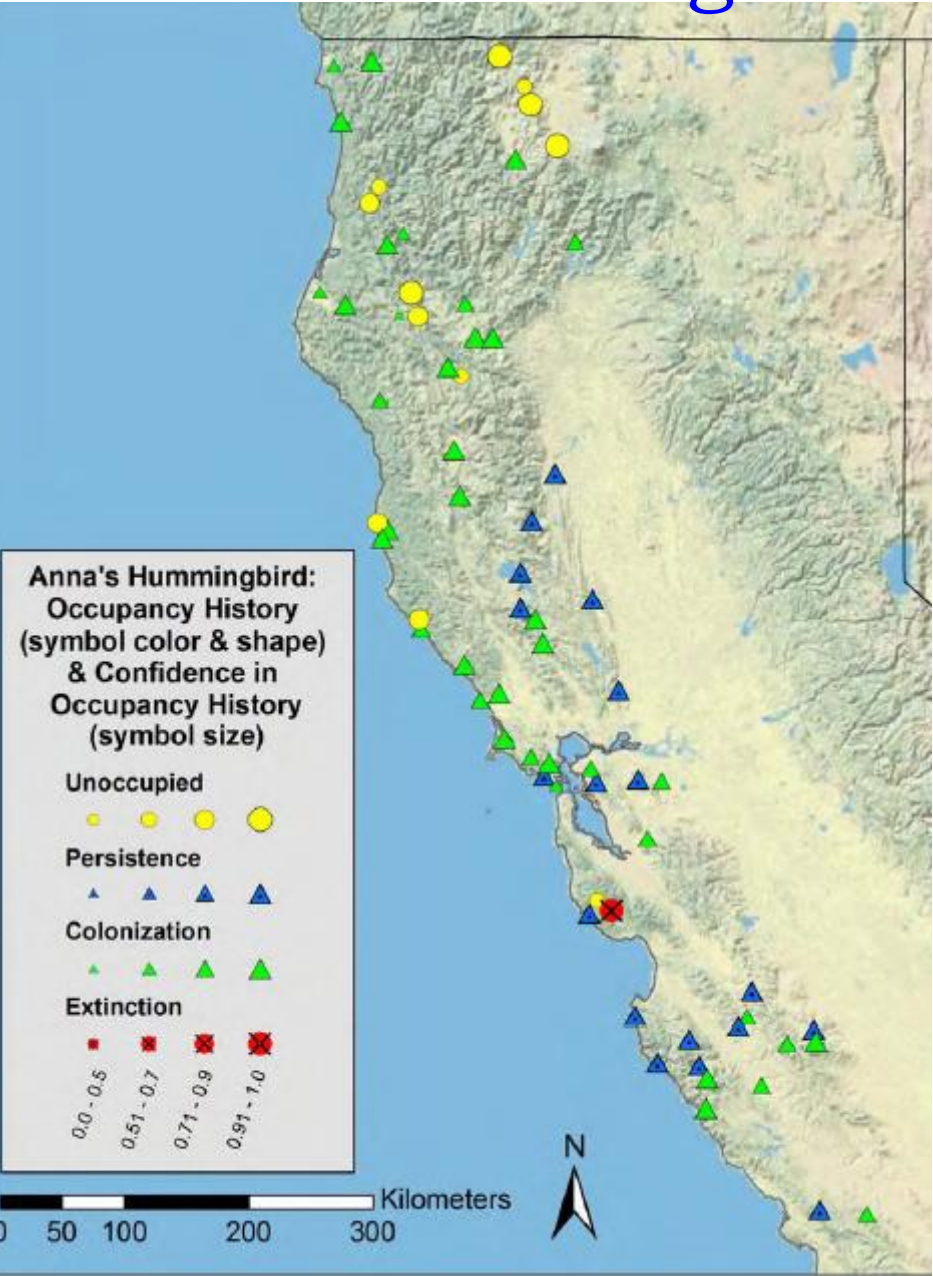
Observer + Julian Day

Observer + Julian Day +
Julian Day * Era

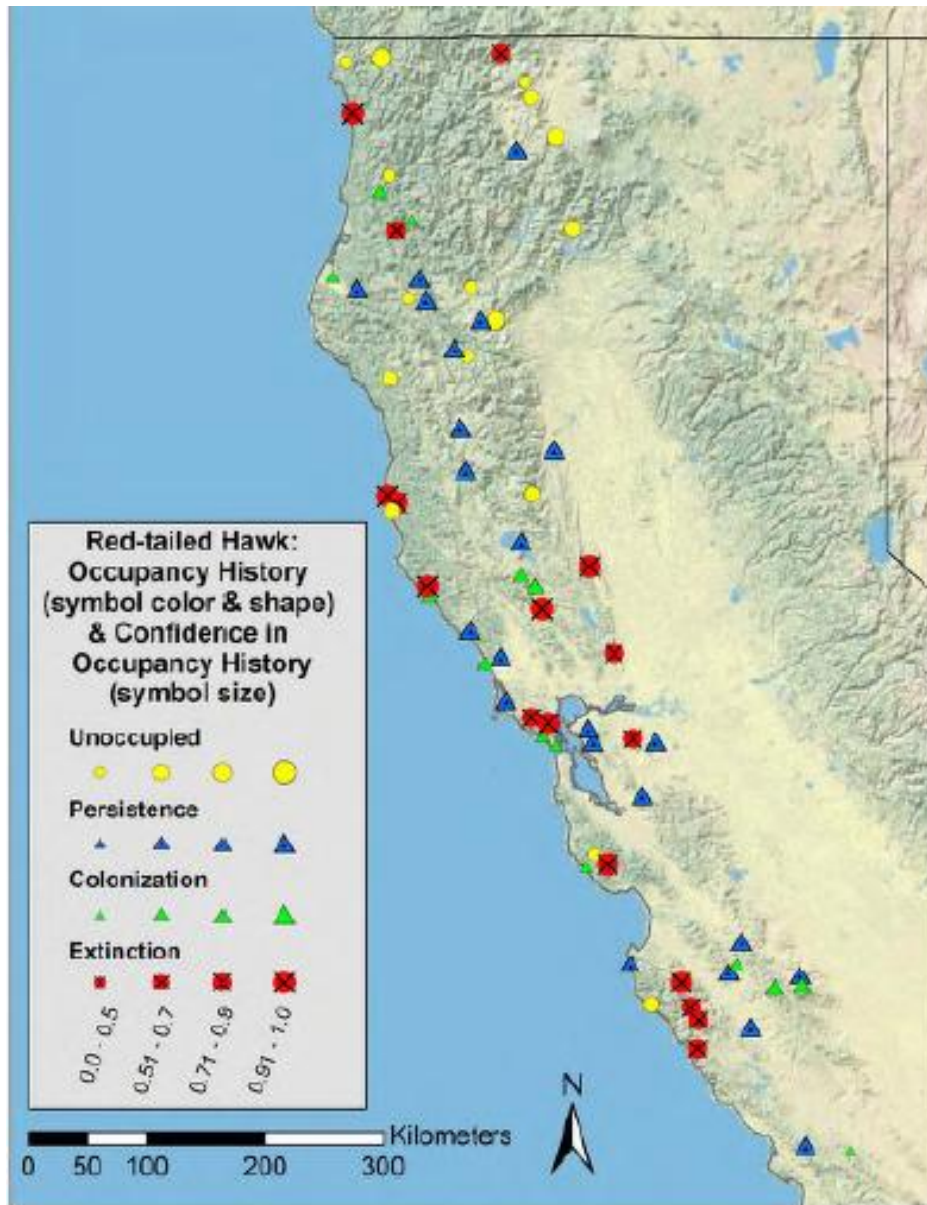
Parameter	Average Cumulative AIC Weight
Observer	0.34
Era	0.89
Julian Day	0.71

Anna's Hummingbird

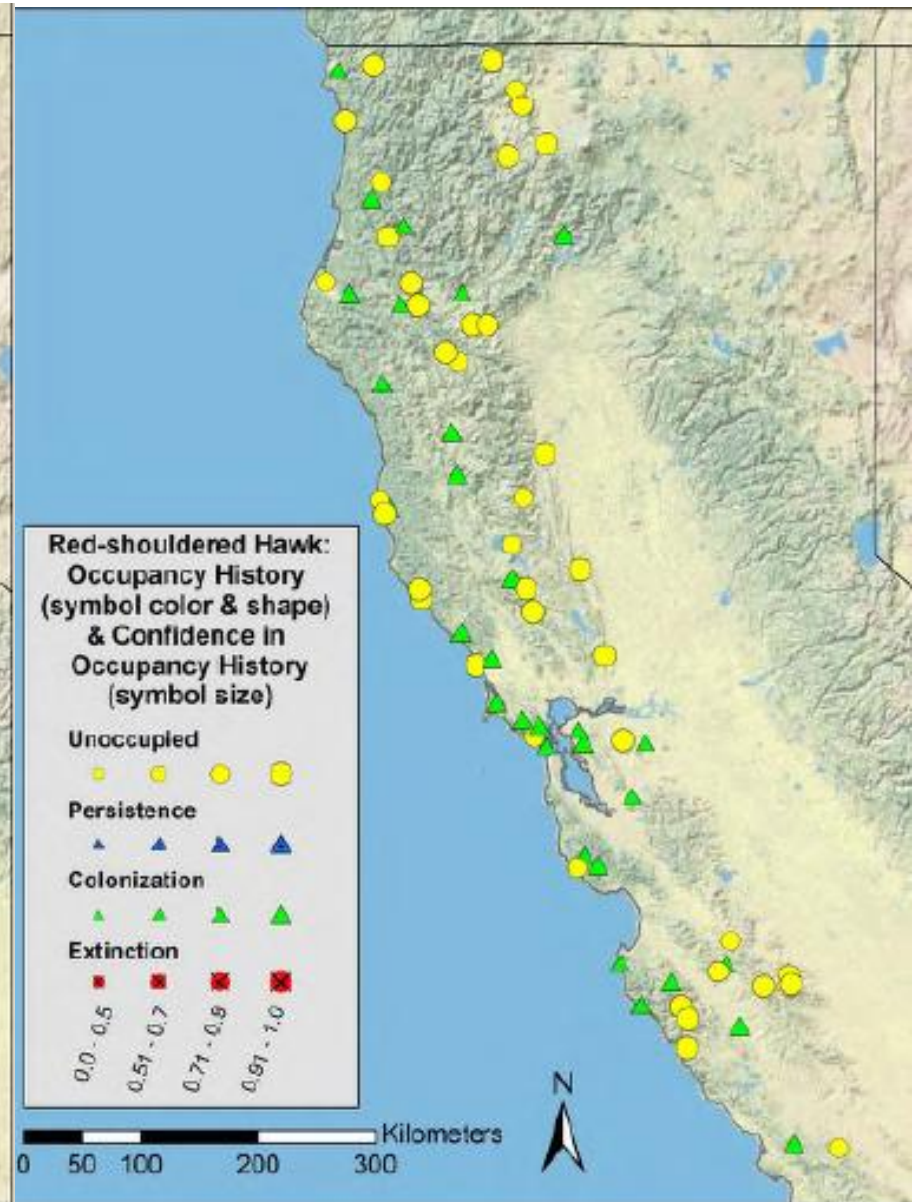
Allen's Hummingbird



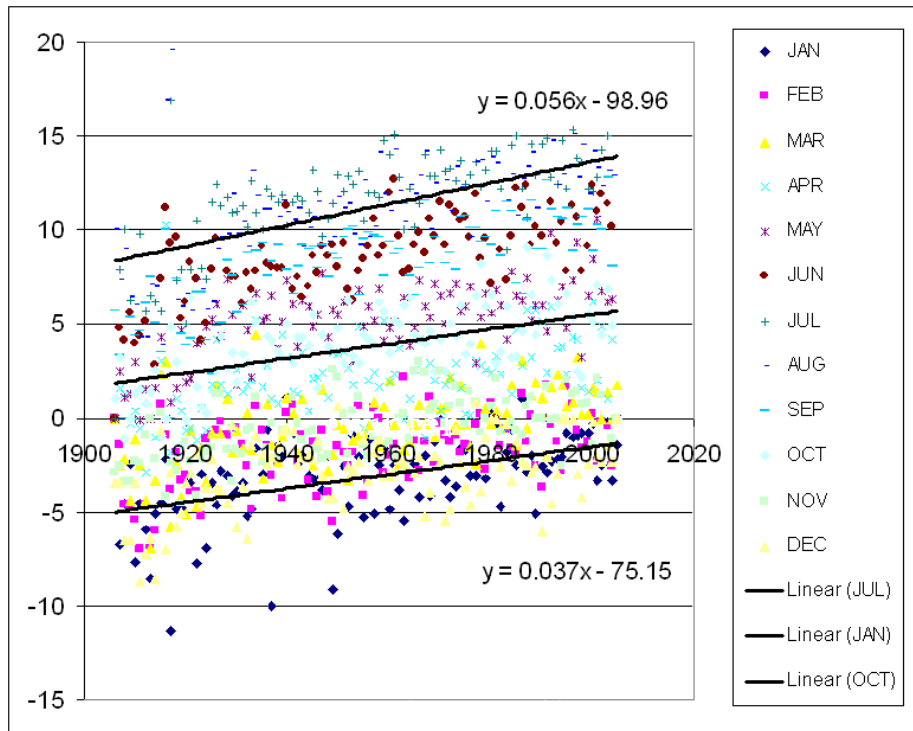
Red-tailed Hawk



Red-shouldered Hawk



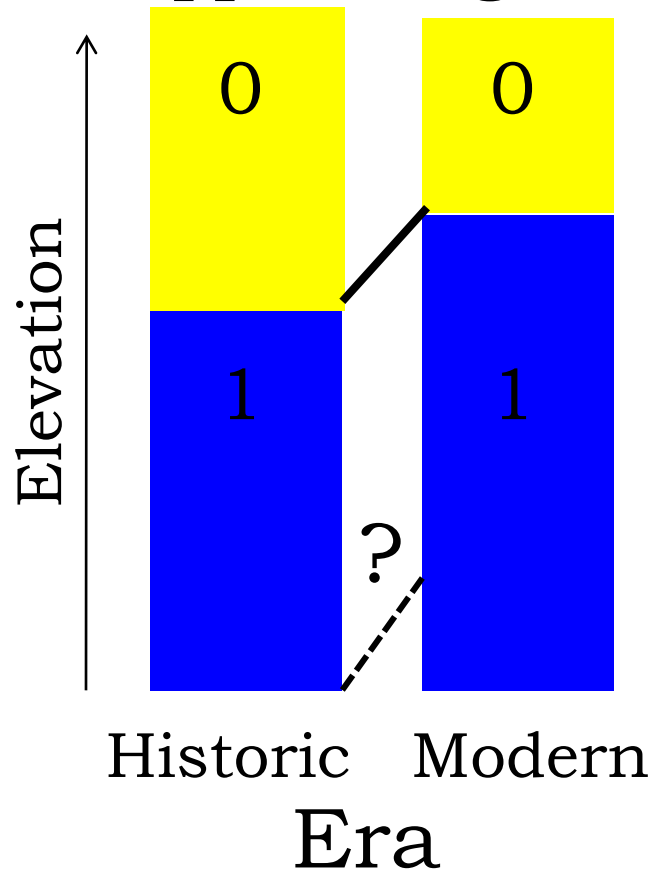
Signatures of Climate Change in Yosemite: Temperature Increase and Glacial Melt



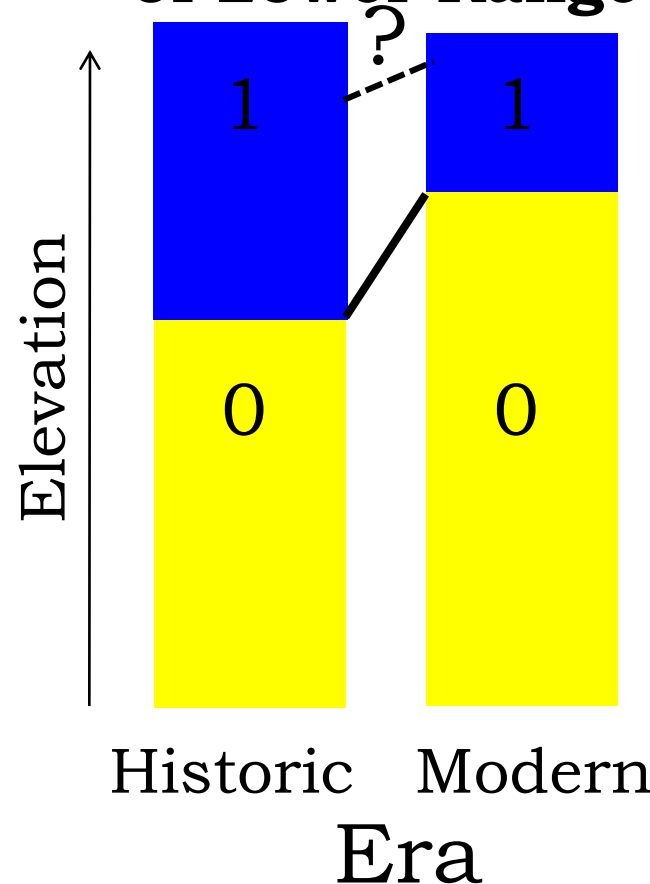
Minimum temperatures of the central Sierras have warmed by 3-4 C over the past 100 years.

Range Change Predictions with Climate Warming

**Low-Mid Elevation
Species: Expansion of
Upper Range**



**Mid-High Elevation
Species: Contraction
of Lower Range**



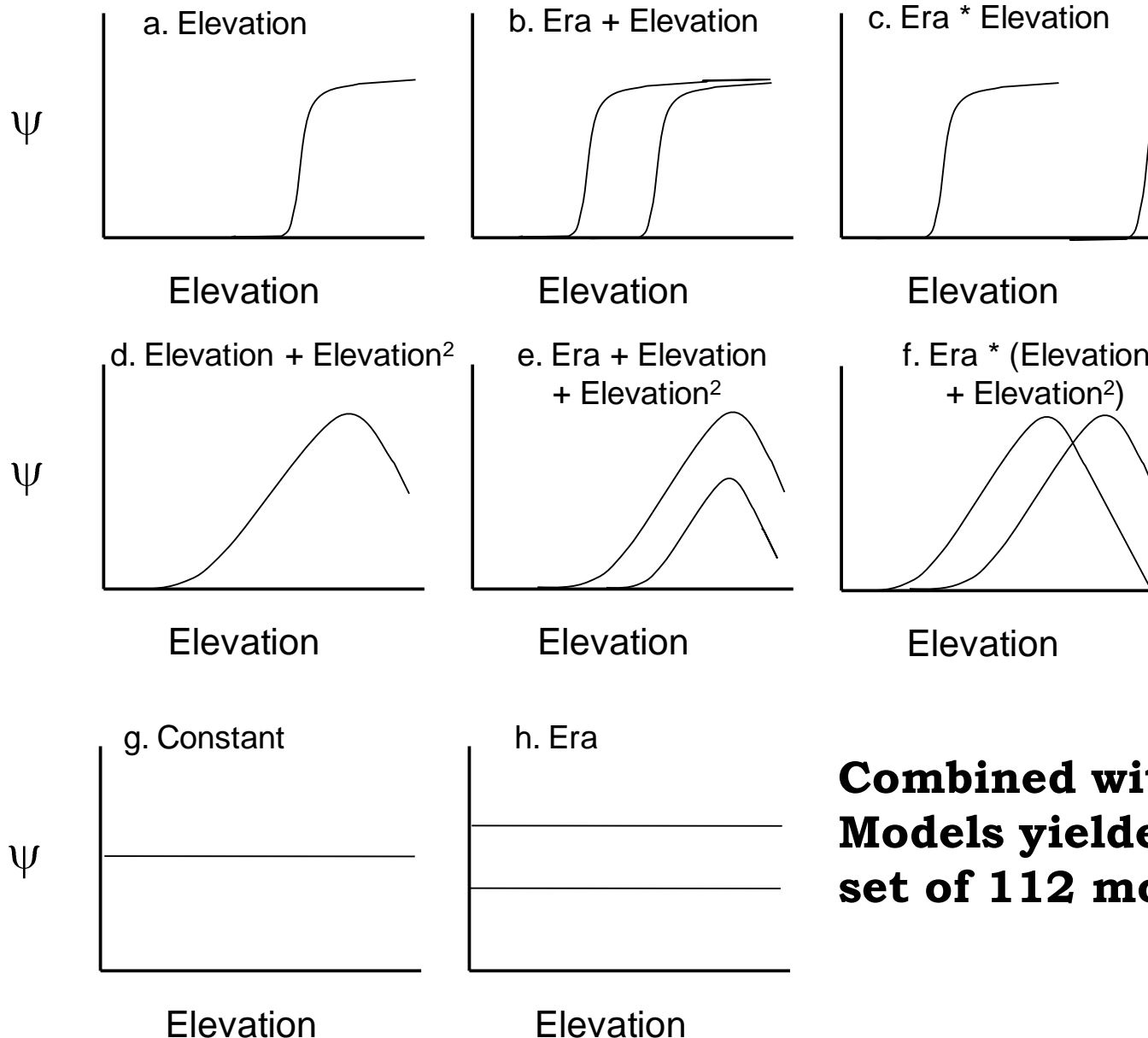
We fit 36 candidate detection models using:

For Mammals:

- **Era** (Grinnell vs. Modern)
- **Trend** (declining success by night)
- **Trapping effort** (mean and log number of traps per night)
- And **combinations** and **interactions** (multiplicative and additive).

The 14 best detection models were used with 8 potential occupancy models with elevation.

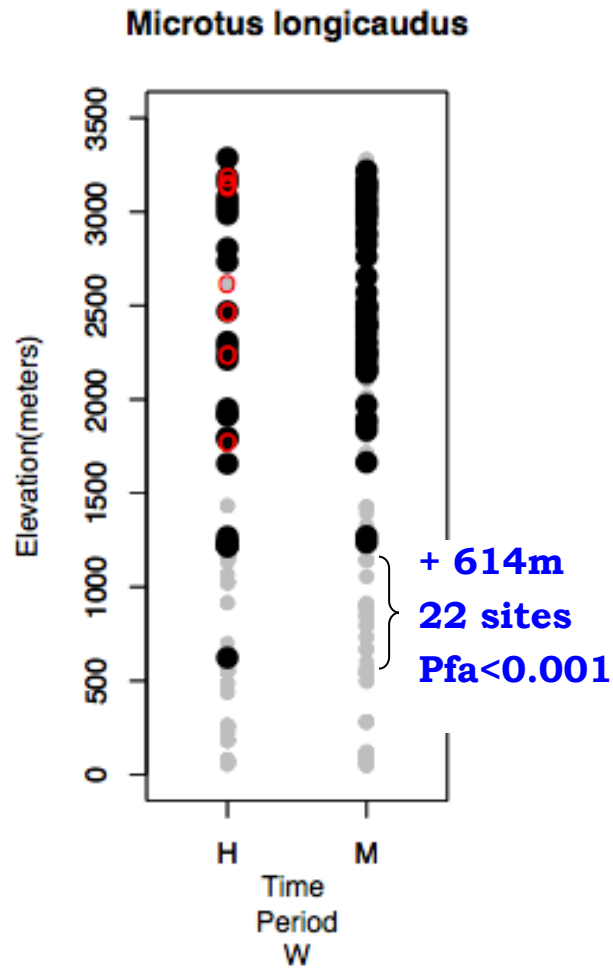
8 Potential Occupancy (Ψ) Models



Combined with 14 detection Models yielded a candidate set of 112 models.



Microtus longicaudus



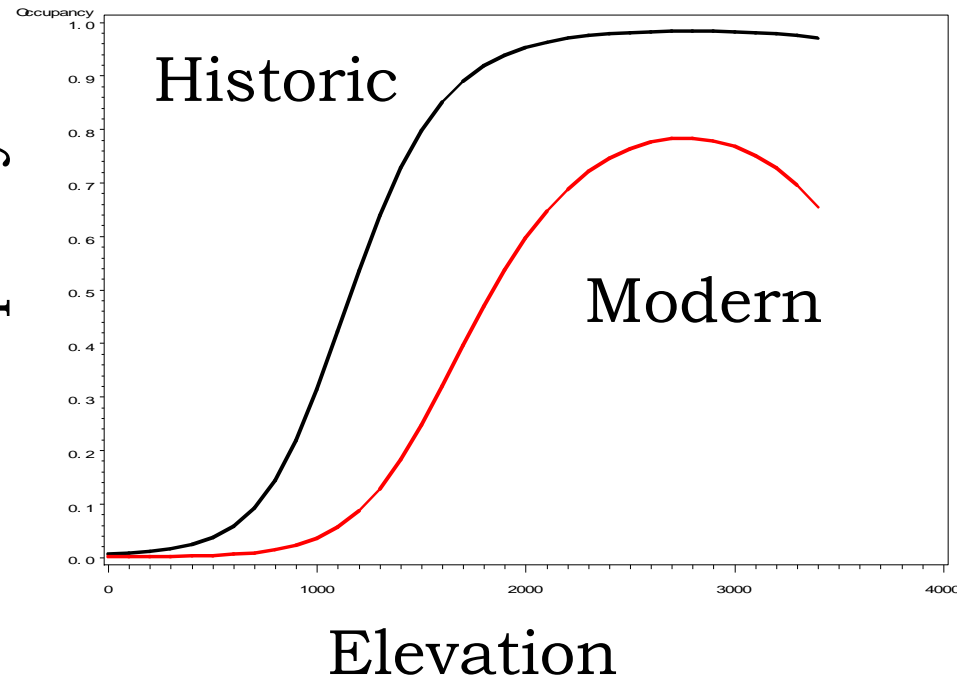
Occupancy models

Cumulative AIC Wt

Constant	0.00
Elev	0.00
Elev+Elev ²	0.00
Era	0.00
Era*(Elev + Elev ²)	0.19
Era*Elev	0.03
Era+Elev	0.04
Era+Elev+Elev ²	0.74

Occupancy of MICROTUS_LONGICAUDUS_W.TXT

Occupancy



Moritz et al. 2008. Science 322:261-264

Trapping Data and Occupancy Profiles

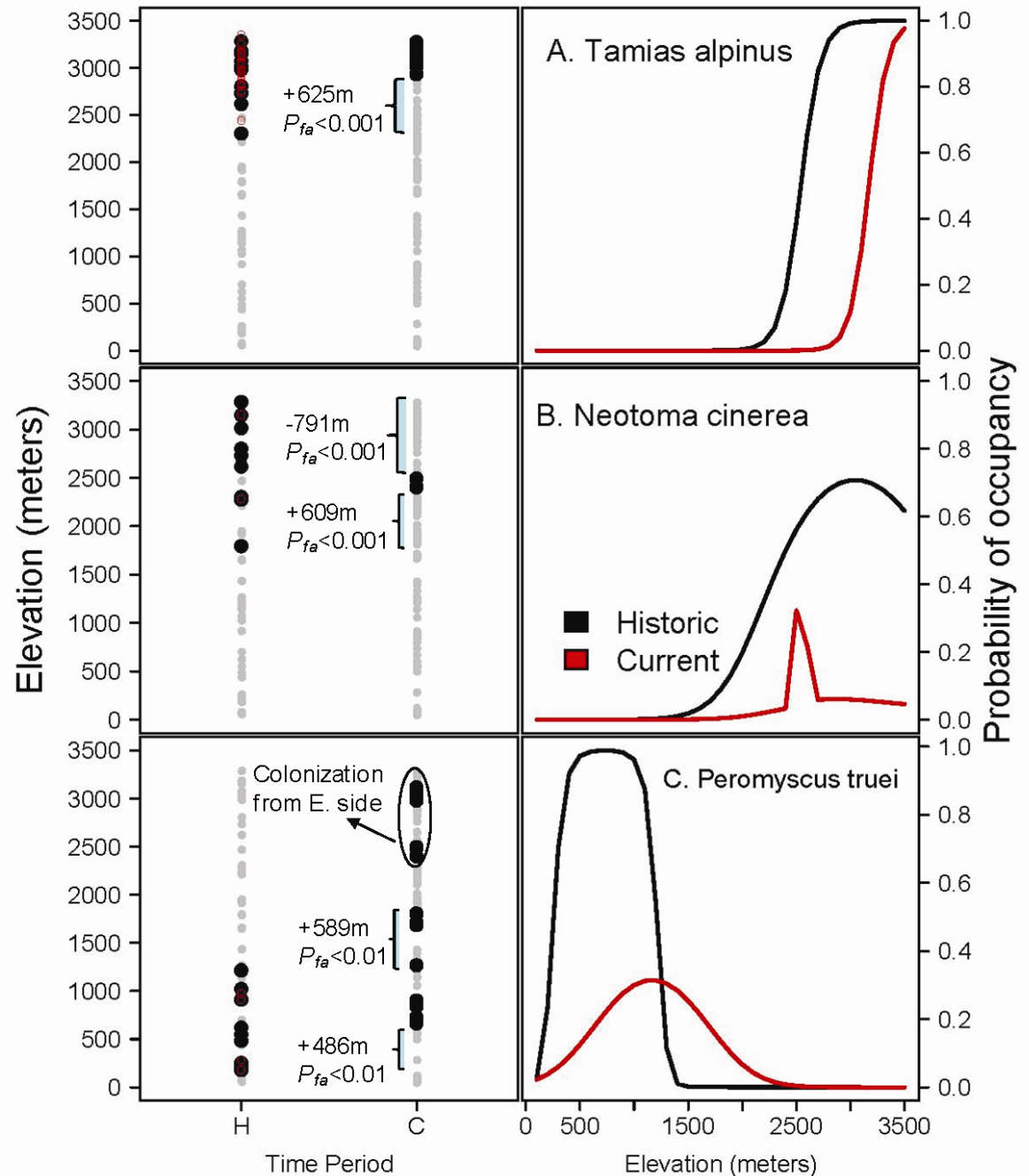
Alpine chipmunk
Tamias alpinus



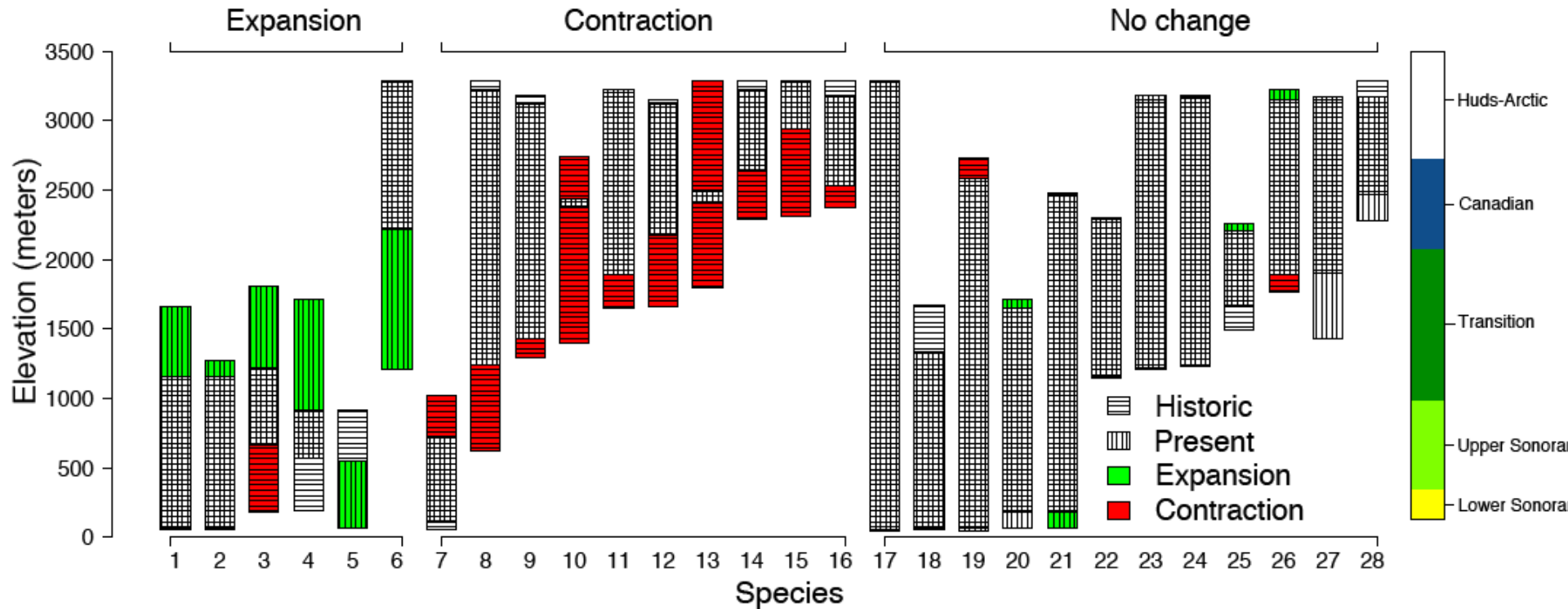
Wood rat
Neotoma cinerea



Piñon mouse
Peromyscus truei



Elevational Range Change for 28 Yosemite Small Mammal Species

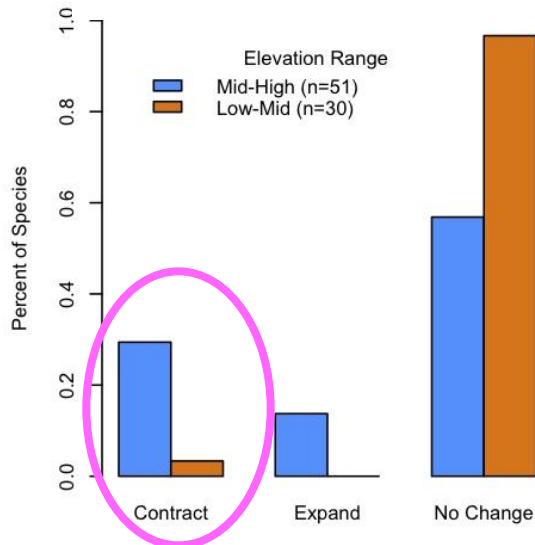


Moritz et al. 2008. Science 322: 261-264.

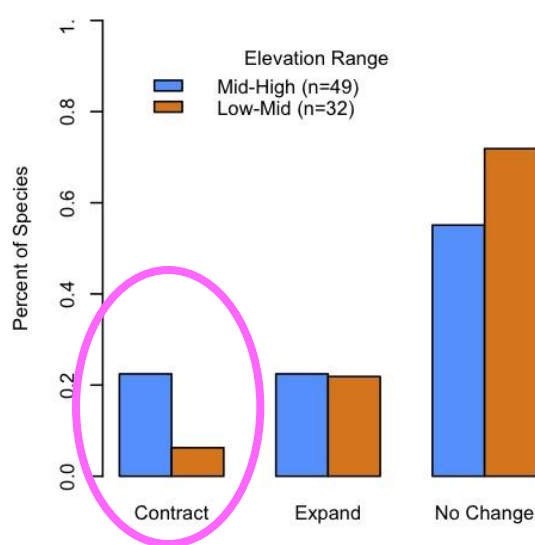
Range Changes in Sierra Birds

Elevation Range: ■ **Mid-High** ■ **Low-Mid Elev.**

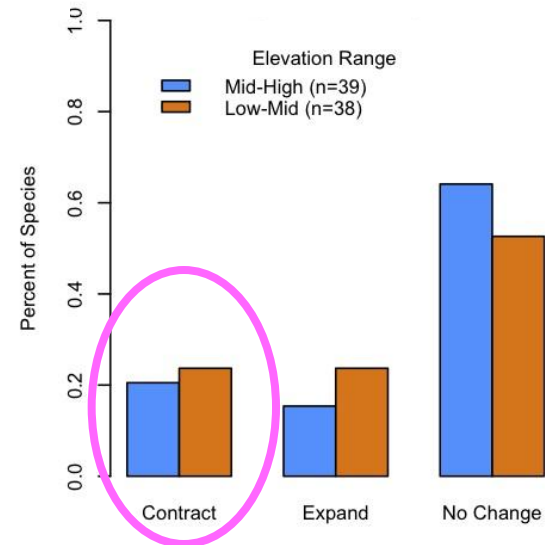
Lassen Lower Limit



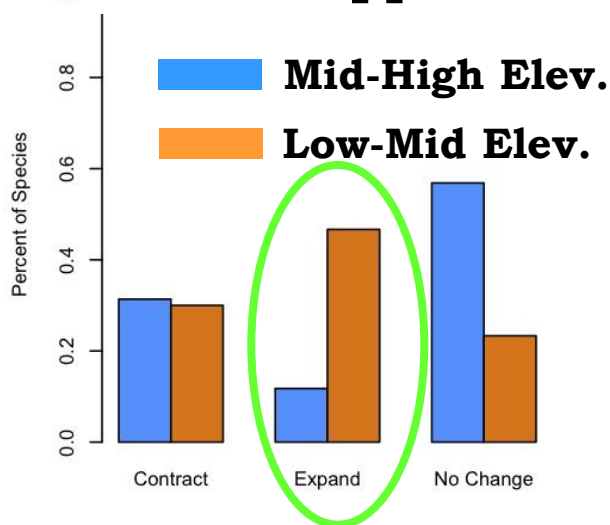
Yosemite Lower Limit



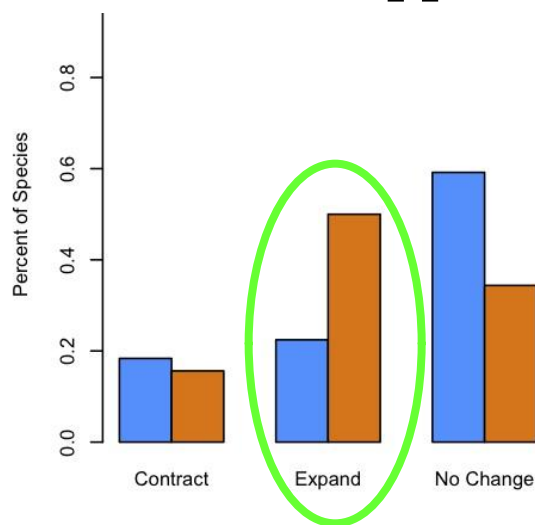
S. Sierra Lower



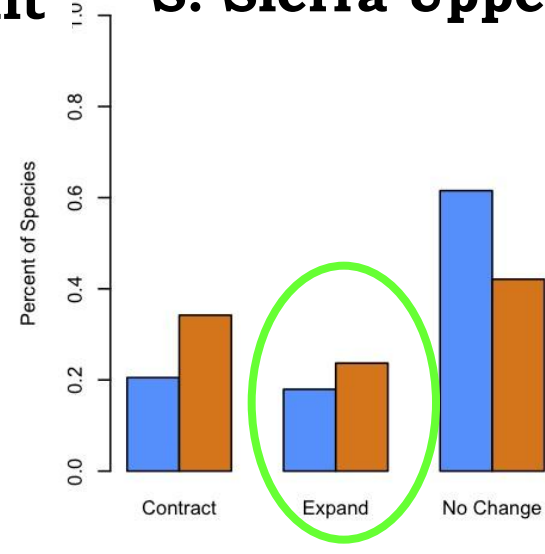
Lassen Upper Limit



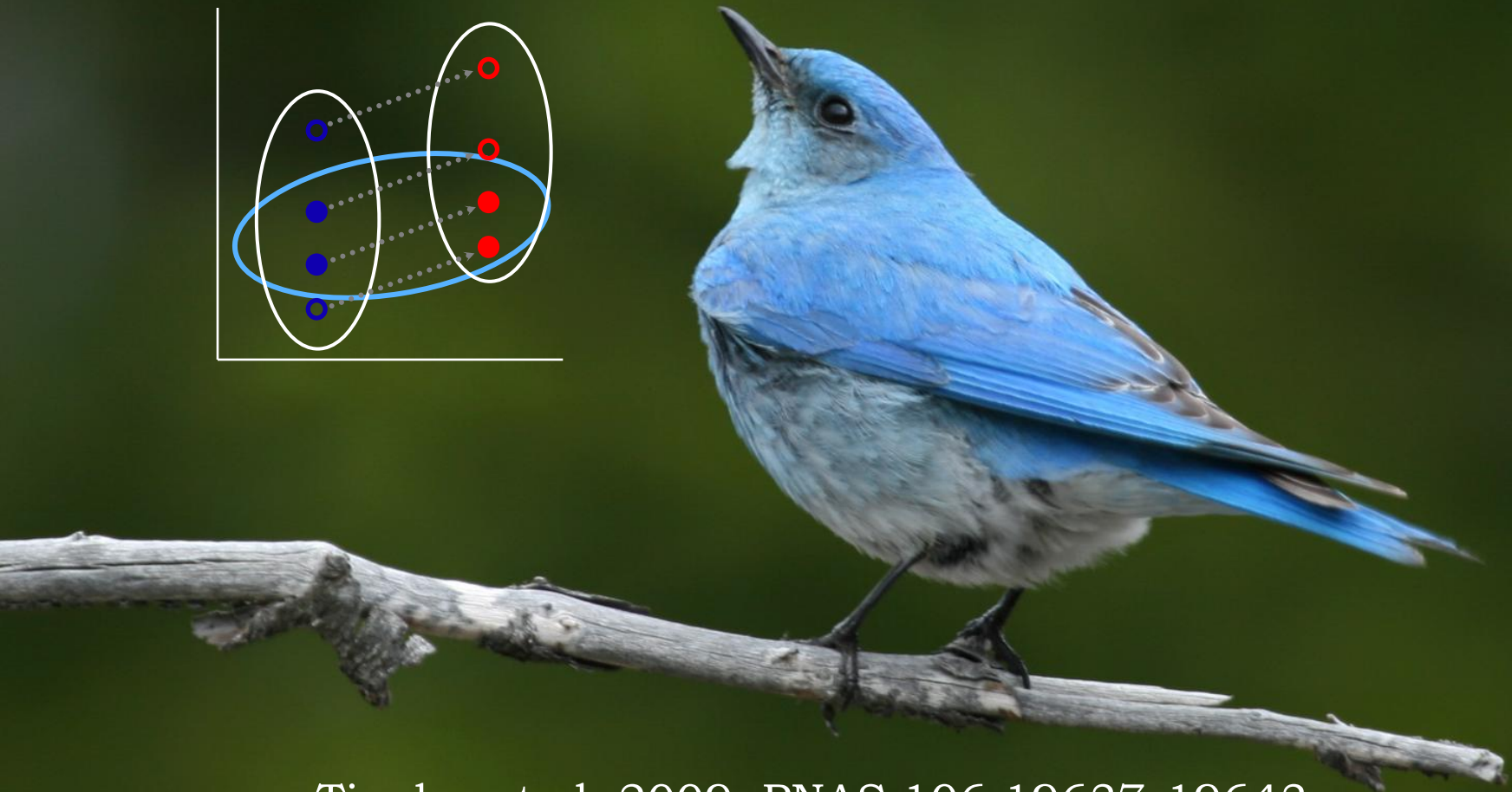
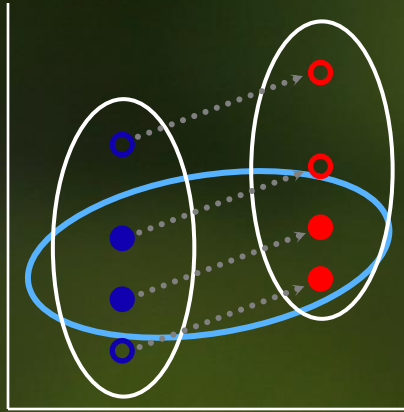
Yosemite Upper Limit



S. Sierra Upper



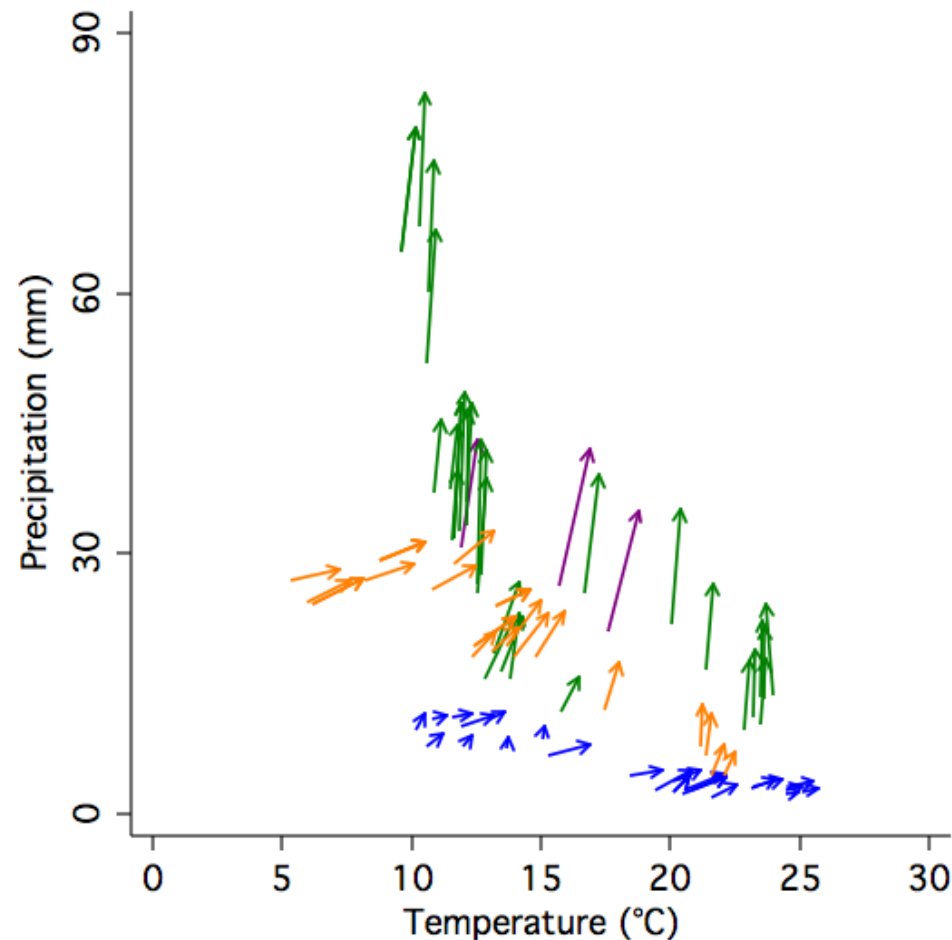
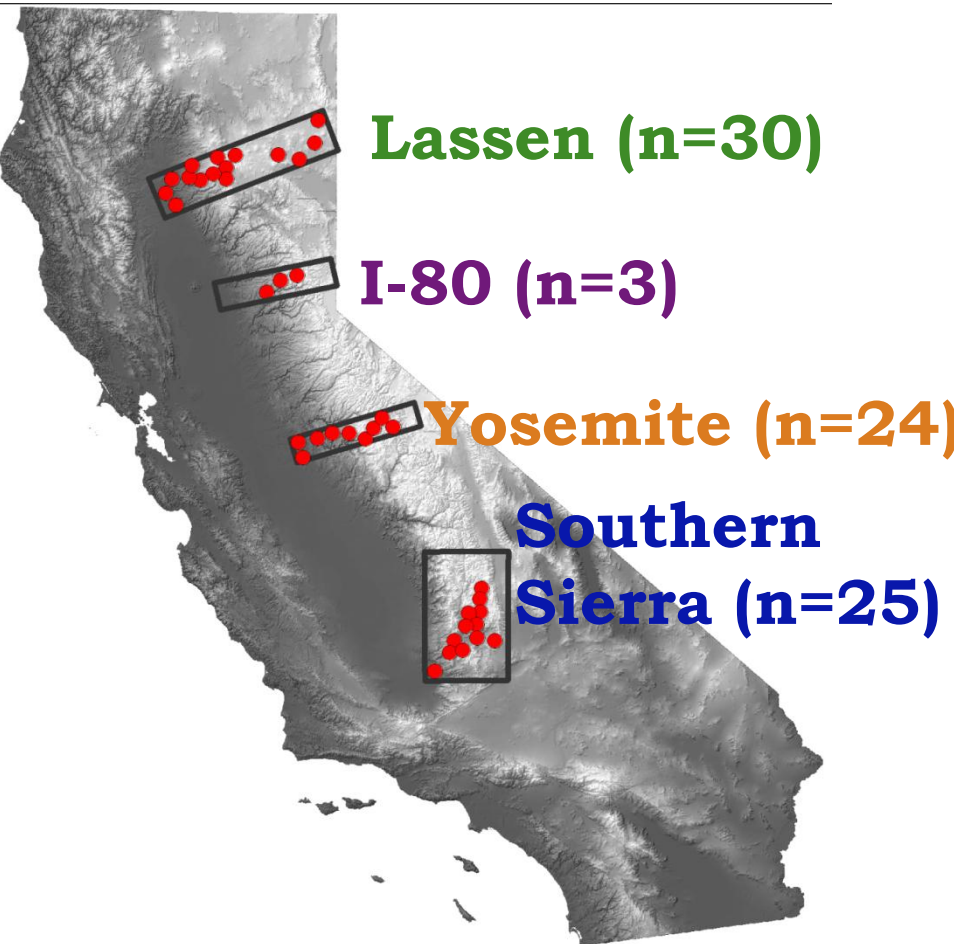
Causation: Do birds track their climatic niche in response to a century of climate change?



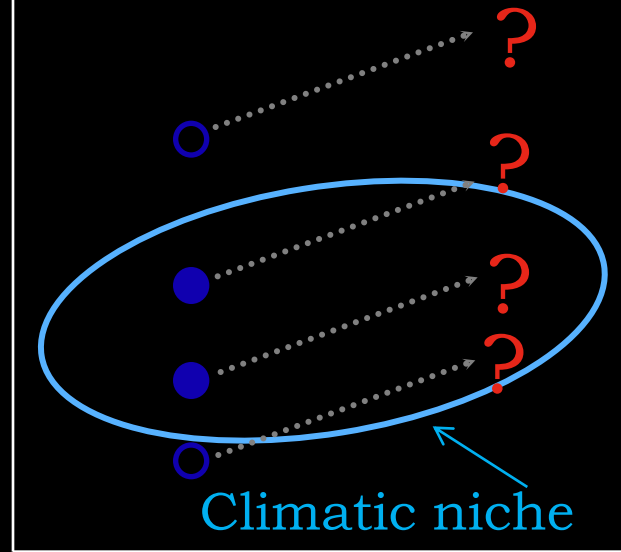
Tingley et al. 2009. PNAS 106:19637-19643.

Grinnell Resurvey Project Transects

Resurveyed and Climate Change Vectors



Precipitation

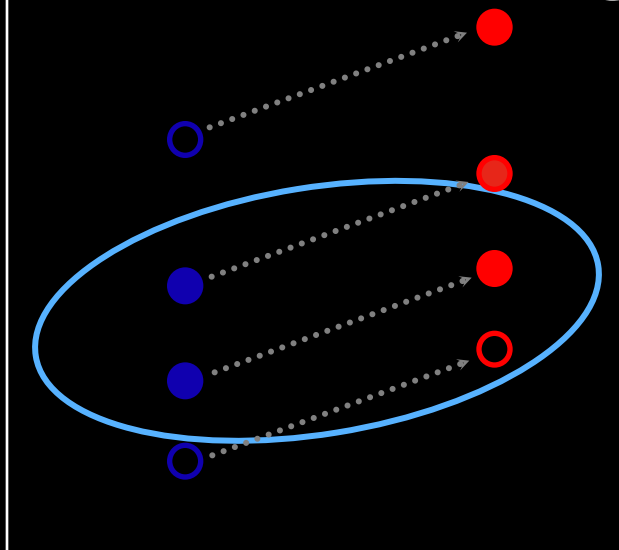


Niche Tracking:
species follow limiting
environmental
boundaries through
geographical space to
remain in favorable
climatic space

Temperature

Not Niche Tracking

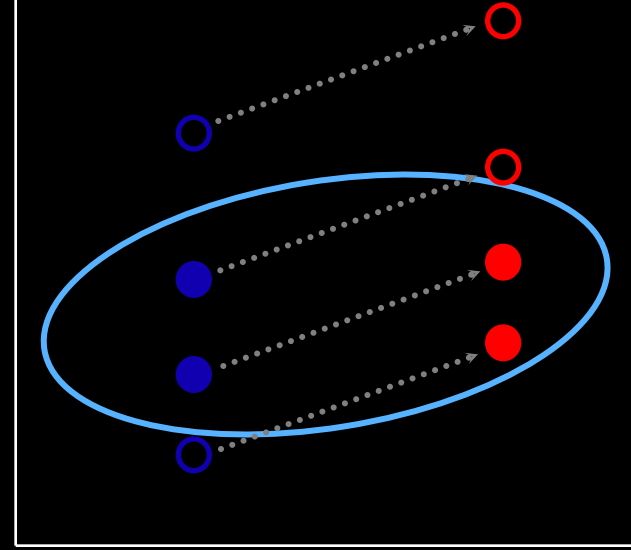
Precipitation



Temperature

Niche Tracking

Precipitation

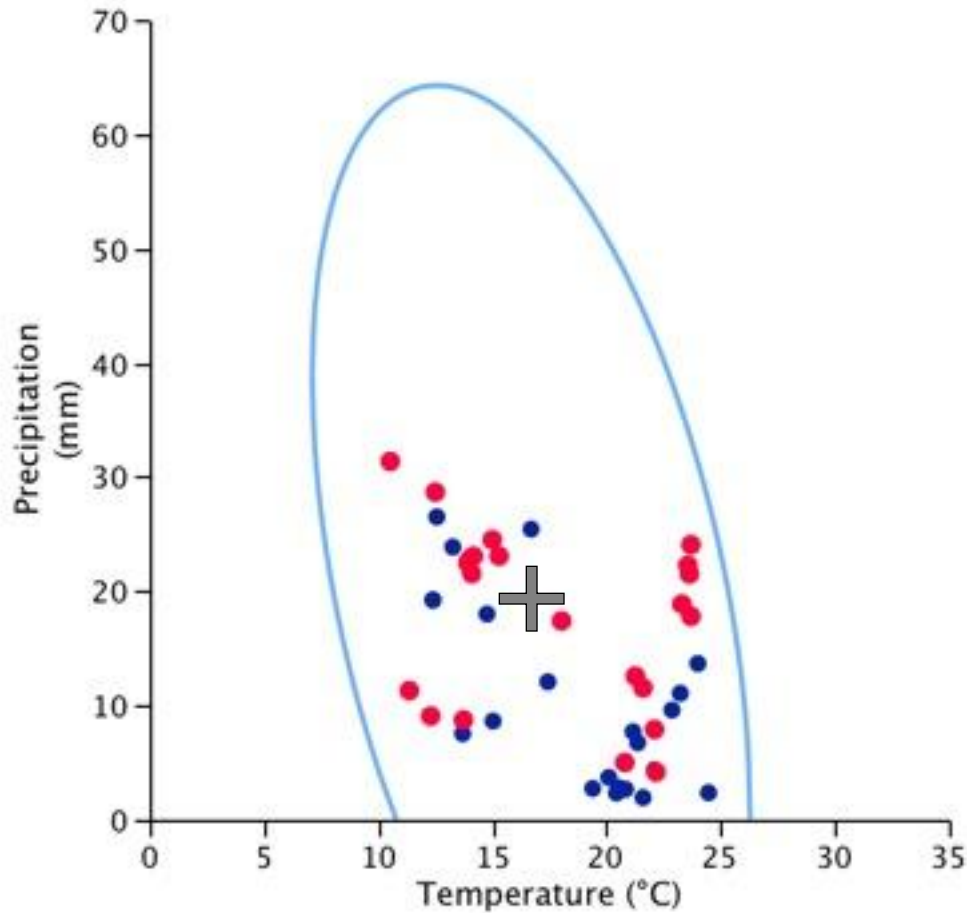


Temperature

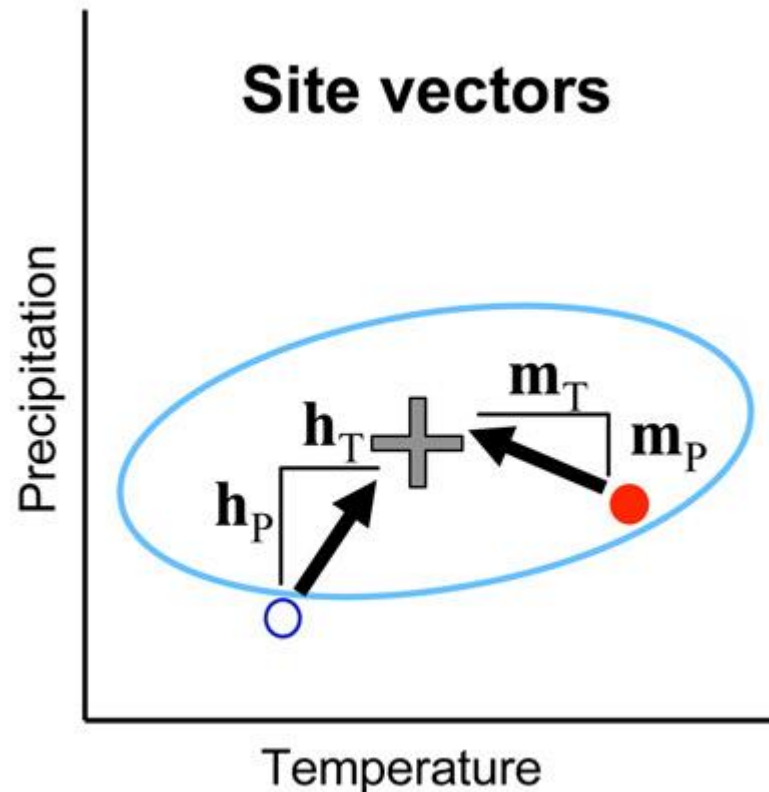
Measuring Niche Tracking



**Specimens
which were**
Historical
(1860 -1940
with
Lat/Longs
breeding
season only



Sites can be defined by vector components describing the position of a site (e.g., site 4) either historically (\mathbf{h}_T and \mathbf{h}_P) or currently (\mathbf{m}_T and \mathbf{m}_P) relative to the **climatic niche centroid**. These site-specific vectors are used in combinations as covariates of colonization and extinction in **Multi-Season Occupancy Models**.



91% of Species (N=53) Niche Tracked

Low elevation

Middle elevation

High elevation

Species	Tracking	Species	Tracking	Species	Tracking
Nuttall's Woodpecker	--	Violet-green Swallow	precip	Mountain Quail	temp
Oak Titmouse	precip	Lazuli Bunting	temp, precip	Dusky Flycatcher	temp
Bullock's Oriole	precip	Lesser Goldfinch	precip	Steller's Jay	temp
California Towhee	precip	Western Scrub-Jay	--	Red-breasted Sapsucker	temp
Acorn Woodpecker	precip	Canyon Wren	precip	White-headed Woodpecker	temp
Western Kingbird	precip	Spotted Towhee	precip	Green-tailed Towhee	temp
California Quail	precip	Black-headed Grosbeak	precip	White-crowned Sparrow	temp, precip
California Thrasher	--	Pacific-slope Flycatcher	temp	Mountain Chickadee	temp
Lark Sparrow	precip	Brewer's Blackbird	precip	Yellow-rumped Warbler	temp, precip
Bewick's Wren	precip	Cassin's Vireo	temp, precip	Townsend's Solitaire	temp
Ash-throated Flycatcher	temp, precip	Black-throated Gray Warbler	temp, precip	Pygmy Nuthatch	precip
Anna's Hummingbird	--	Northern Flicker	temp, precip	Hammond's Flycatcher	temp, precip
Bushtit	precip	Rock Wren	temp	Cassin's Finch	temp
Western Meadowlark	precip	Western Wood-Pewee	temp, precip	American Dipper	temp
Black Phoebe	--	Hermit Warbler	precip	Williamson's Sapsucker	temp, precip
Wrentit	precip	Western Tanager	temp, precip	Mountain Bluebird	temp, precip
Lawrence's Goldfinch	precip	MacGillivray's Warbler	temp, precip	Clark's Nutcracker	temp
Western Bluebird	temp, precip	Calliope Hummingbird	precip		

Species' elevation significantly associated with tracked gradient ($F_{3,49}=20.4$, $P<0.001$)

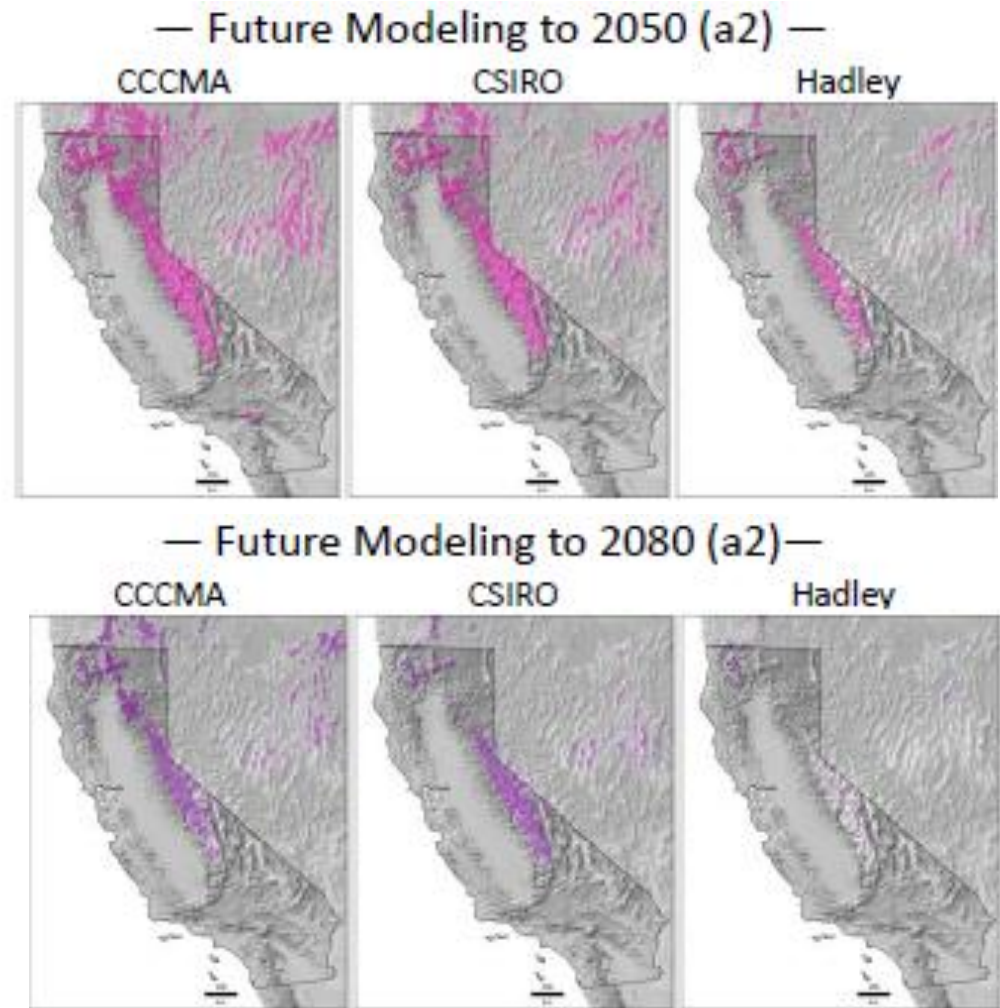
The 5 species that did not track their climate niche were urban colonists.

Species	Tracking	Species	Tracking	Species	Tracking
Nuttall's Woodpecker	--	Violet-green Swallow	precip	Mountain Quail	temp
Oak Titmouse	precip	Lazuli Bunting	temp, precip	Dusky Flycatcher	temp
Bullock's Oriole	precip	Lesser Goldfinch	precip	Steller's Jay	temp
California Towhee	precip	Western Scrub-Jay	--	Red-breasted Sapsucker	temp
Acorn Woodpecker	precip	Canyon Wren	precip	White-headed Woodpecker	temp
Western Kingbird	precip	Spotted Towhee	precip	Green-tailed Towhee	temp
California Quail	precip	Black-headed Grosbeak	precip	White-crowned Sparrow	temp, precip
California Thrasher	--	Pacific-slope Flycatcher	temp	Mountain Chickadee	temp
Lark Sparrow	precip	Brewer's Blackbird	precip	Yellow-rumped Warbler	temp, precip
Bewick's Wren	precip	Cassin's Vireo	temp, precip	Townsend's Solitaire	temp
Ash-thr. Flycatcher	temp, precip	Black-thr. Gray Warbler	temp, precip	Pygmy Nuthatch	precip
Anna's Hummingbird	--	Northern Flicker	temp, precip	Hammond's Flycatcher	temp, precip
Bushtit	precip	Rock Wren	temp	Cassin's Finch	temp
Western Meadowlark	precip	Western Wood-Pewee	temp, precip	American Dipper	temp
Black Phoebe	--	Hermit Warbler	precip	Williamson's Sapsucker	temp, precip
Wrentit	precip	Western Tanager	temp, precip	Mountain Bluebird	temp, precip
Lawrence's Goldfinch	precip	MacGillivray's Warbler	temp, precip	Clark's Nutcracker	temp
Western Bluebird	temp, precip	Calliope Hummingbird	precip		

Species Distribution Models use climate to project occupancy (*Callospermophilus lateralis*)



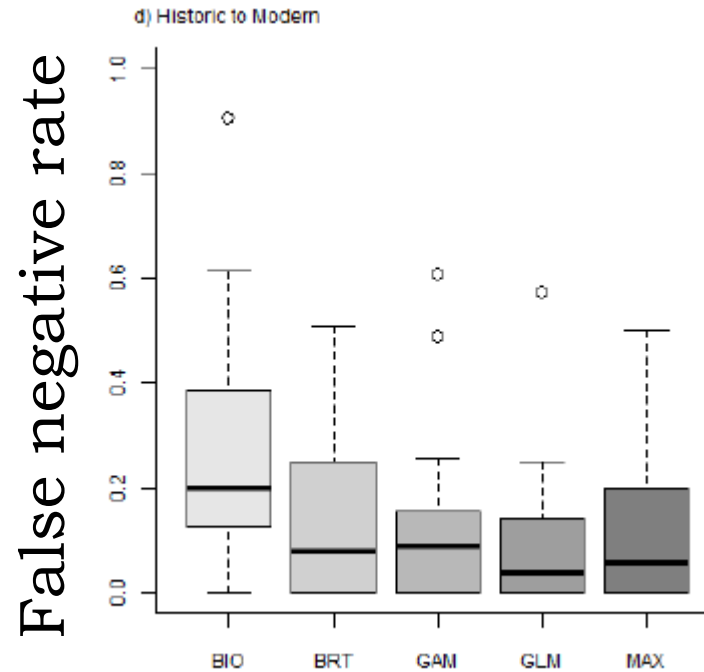
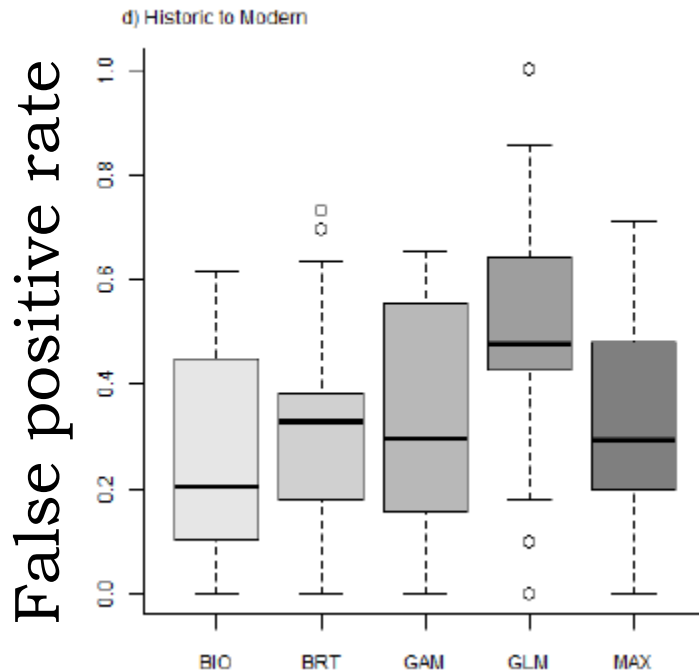
Golden-mantled ground squirrel



Species distribution models (SDMs) over-predict presence more often than absence.

Mean = 0.35

Mean = 0.14



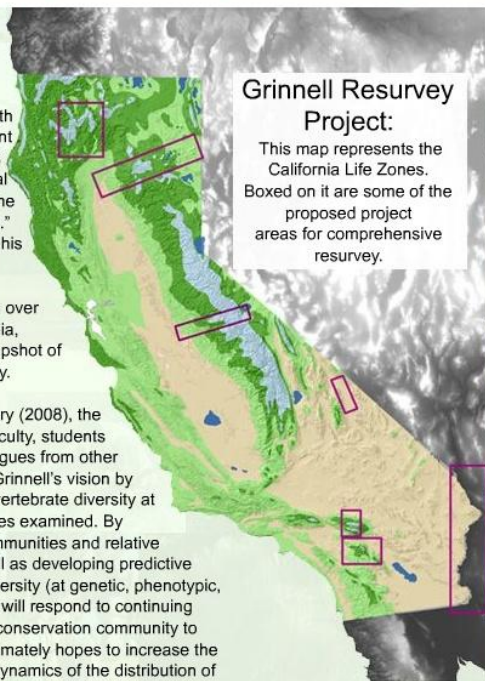
SDMs that had good predictive performance for historic data did not perform well in projecting contemporary occupancy.

Conclusions

- 1. Someone has already walked where you walked – look for historic data to incorporate into your monitoring program.**
- 2. Occupancy models have a central role to play in quantifying the impacts of climate change on range shifts and extinctions.**
- 3. Elevation range changes in Sierra Nevadan small mammals and birds over the past 100 years mostly support patterns predicted by climate change, but species responses were idiosyncratic and much important spatial variation exists.**
- 4. Birds appear to track changes in their bioclimatic niche and niche models had disappointing accuracy in projecting across the last 100 years, providing mixed support for their use to project future range shifts under climate change scenarios.**

Nearly a century ago, Joseph Grinnell began his career as the founding Director of the Museum of Vertebrate Zoology (MVZ) with this vision: "...That the student of the future will have access to the original record of faunal conditions in California and the west, wherever we now work." To realize this vision, he and his colleagues documented and collected mammals, birds, amphibians and reptiles from over 700 locations across California, resulting in a remarkable snapshot of early 20th century biodiversity.

As it approaches its Centenary (2008), the MVZ, through research by faculty, students and staff together with colleagues from other institutes, intends to further Grinnell's vision by extensively resurveying the vertebrate diversity at the sites he and his colleagues examined. By documenting changes in communities and relative abundance of species as well as developing predictive models of how vertebrate diversity (at genetic, phenotypic, species & community levels) will respond to continuing change and efforts from the conservation community to protect diversity, the MVZ ultimately hopes to increase the understanding of long-term dynamics of the distribution of vertebrates in California.



Grinnell Resurvey Project:

This map represents the California Life Zones. Boxed on it are some of the proposed project areas for comprehensive resurvey.



mvz.berkeley.edu/Grinnell/

cnr.berkeley.edu/~beis/BeissingerLab

Thanks!

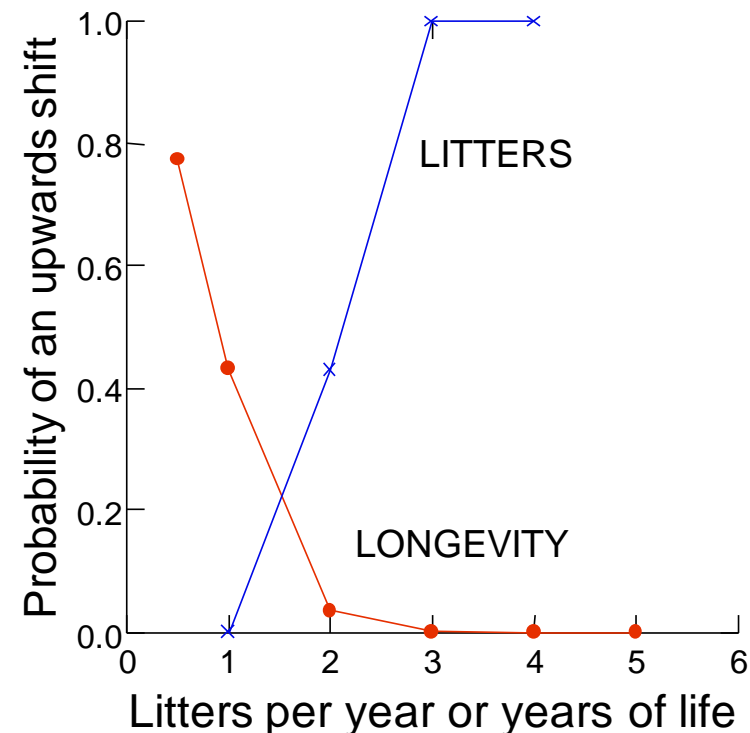


Which Mammal Species Moved?

1. Closely-related and ecologically-similar species responded idiosyncratically.

2. Lower Range Limit - Life Zone was the best predictor of a change.

3. Upper Range Limit - Life Zone, Longevity and Litter Size were the best predictors of a shift.



Multiple-Season Occupancy Models (MacKenzie et al. 2002, 2006)

$$\Psi_t = \Psi_{t-1} (1 - \varepsilon_{t-1}) + (1 - \Psi_{t-1}) \gamma_{t-1}$$

Occupied Undetected Not extinct

Unoccupied Colonized

Detected

$$Pr(\mathbf{h}_2 = 000010) = \varphi_1 \prod_{j=1}^3 (1 - p_{1,j}) (1 - \varepsilon) + (1 - \varphi_1) \delta_1 x (1 - p_{2,1}) p_{2,2} (1 - p_{2,3})$$

**Our sites on
public lands
experienced
little
change.**

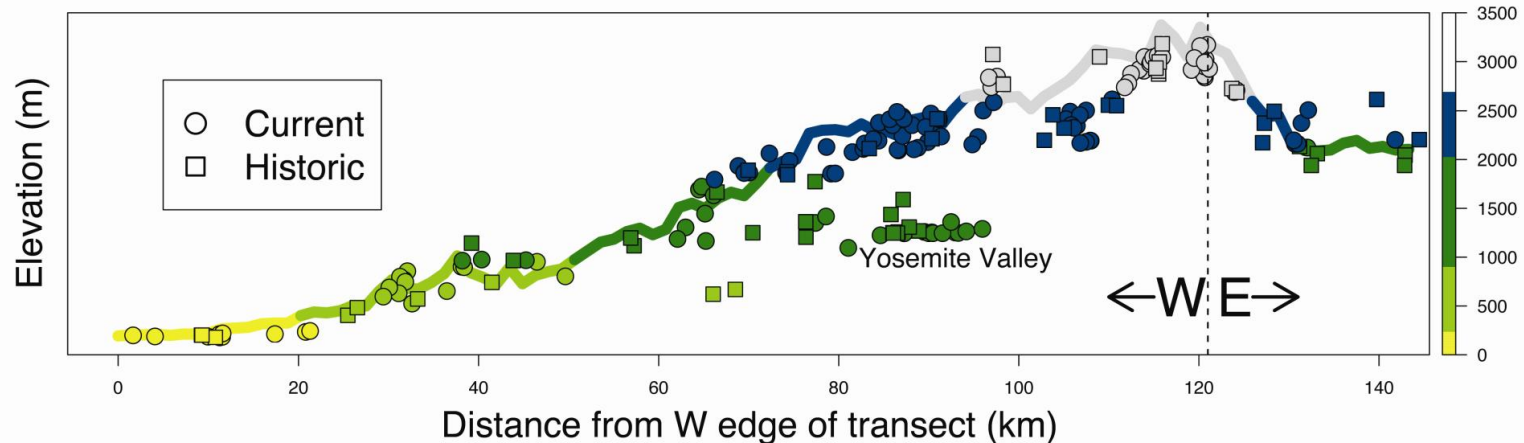
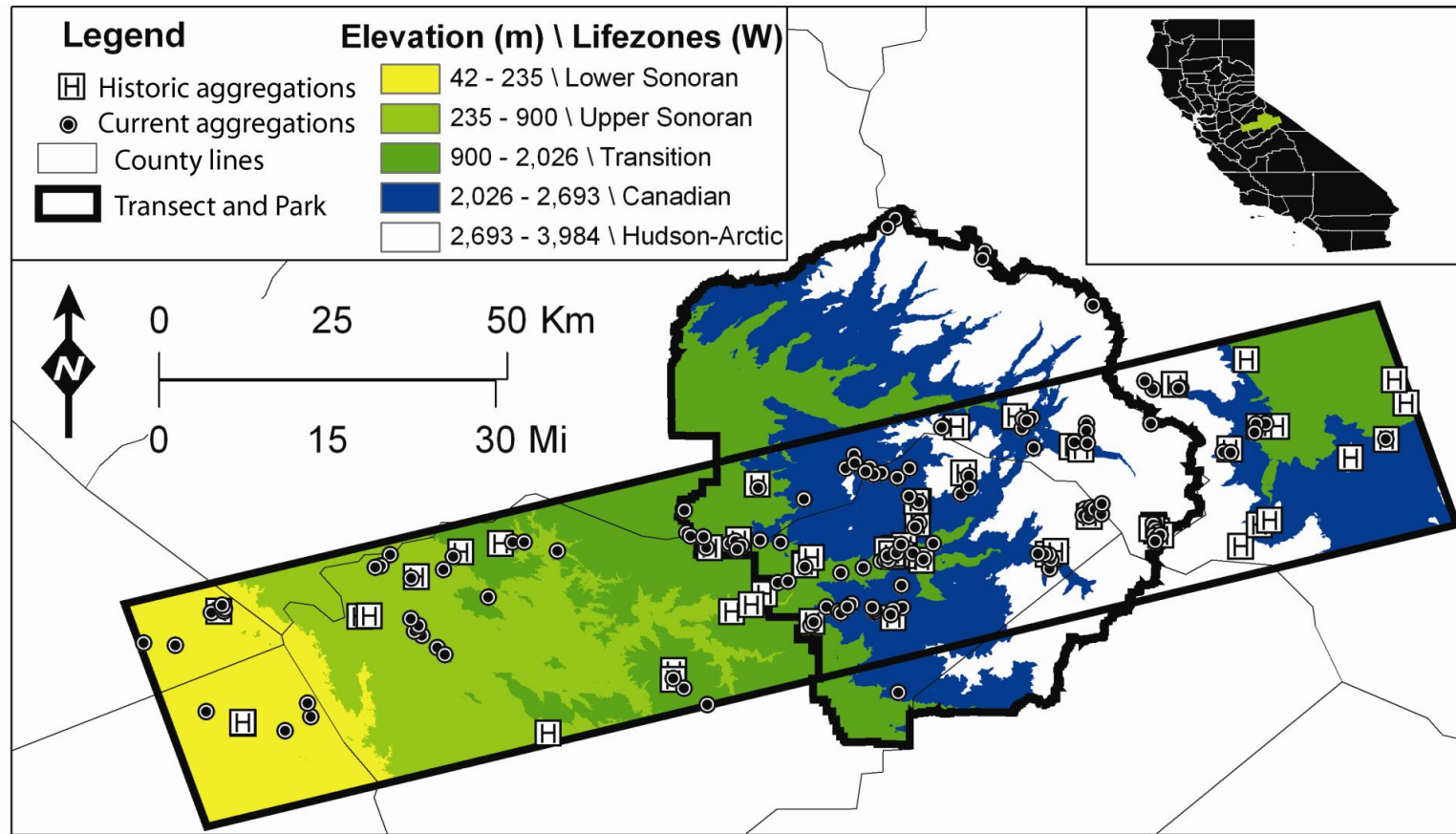
Vogelsang Lake

Note increased
density and
stature of
white-bark pines

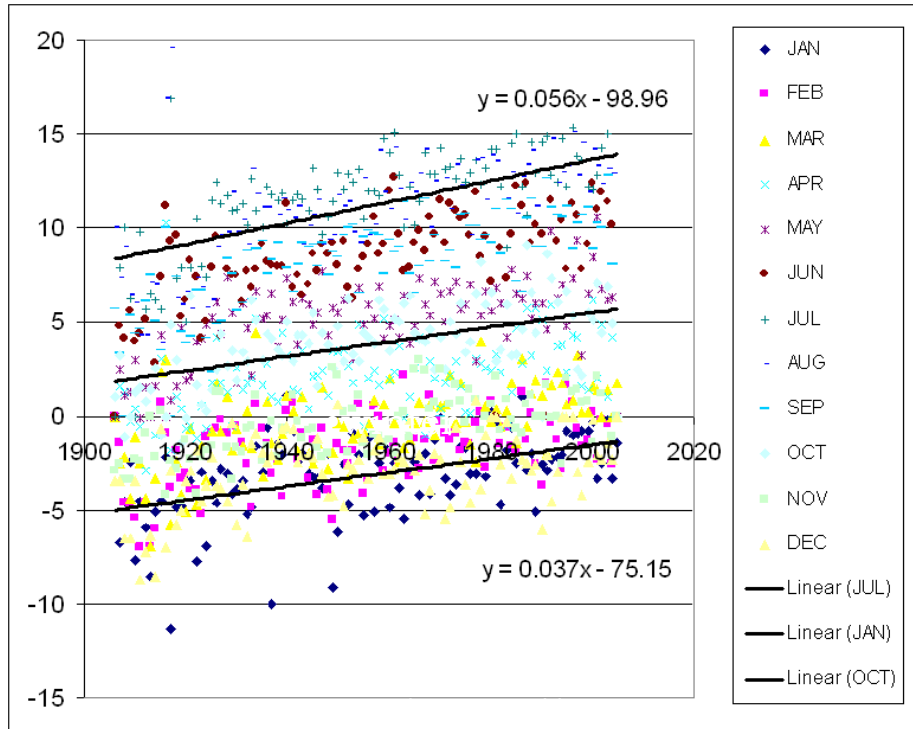


<u>Extent of occurrence data</u>	<u>Data depiction</u>		<u>Nondetection data</u>	<u>Temporal replication</u>	<u>Inference available</u>	<u>Biases to range estimation</u>
	<i>Survey₁</i>	<i>Survey₂</i>				
Presence-only	<i>Site_i</i> ●	—	No	No	Extinction only	Pseudo-absence data leads to overprediction of historical range and of extinction, and no inference on colonization
	<i>Site_j</i> ●	—				
	<i>Site_k</i> —	—				
Presence and non-detection	●	—	Yes	No	Extinction and colonization	False absences give under prediction of historical range and of extinction, and over prediction of colonization
	●	—				
	○	—				
Presence and estimable absence	●	●	Yes	Yes	Extinction and colonization	Probability of occupancy reduces false absence bias
	●	○				
	○	●				
Abundance	④	②	Yes	Yes	Extinction, colonization and change in population size	False absence bias reduced, but abundance comparisons bring new set of biases
	①	○				
	○	③				

Yosemite Transect

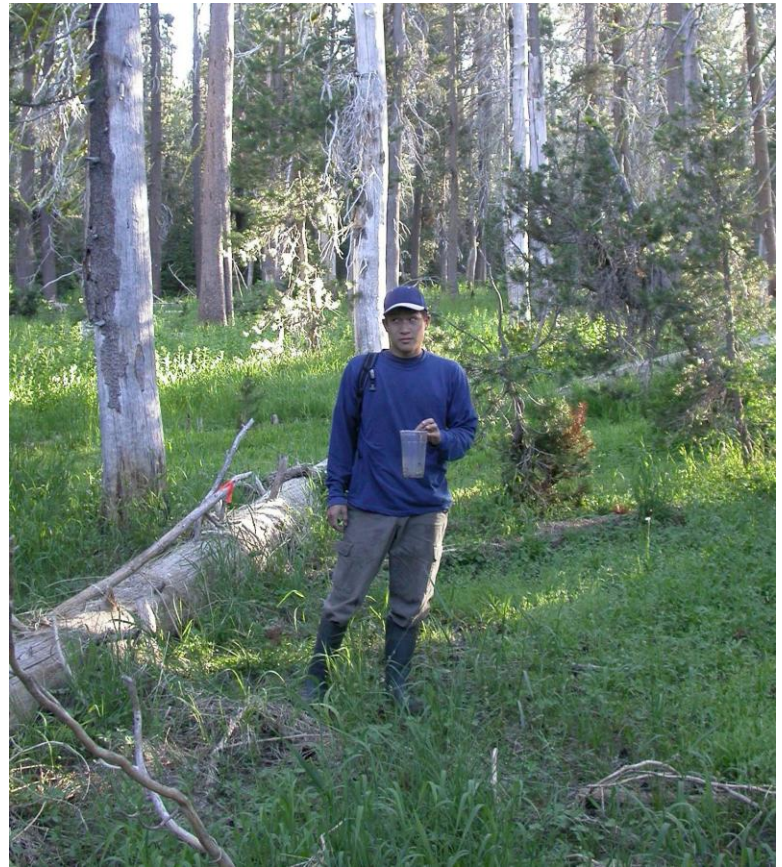


Signatures of Climate Change in Yosemite: Temperature Increase and Glacial Melt



The central Sierra has warmed by 3-4 C over the past 100 years!

Small Mammal Surveys (Jim Patton, Chris Conroy, & undergraduates)



Single Season Occupancy Models

For a series of species' presences (1) and absences (0) observed in repeated surveys at each site: h_1, h_2, \dots, h_s (1,0,1,0,0,0)

$$L(\psi, p | h_1, h_2, \dots, h_s) = \left[\psi^{n_{\cdot}} \prod_{t=1}^T p_t^{n_t} (1 - p_t)^{n_{\cdot} - n_t} \right] \times \left[\psi \prod_{t=1}^T (1 - p_t) + (1 - \psi) \right]^{N - n_{\cdot}}$$

where:

ψ - the probability a species is present (occupancy)

p - the probability of detection

N - the total number of sites surveyed

T - the number of distinct sampling occasions

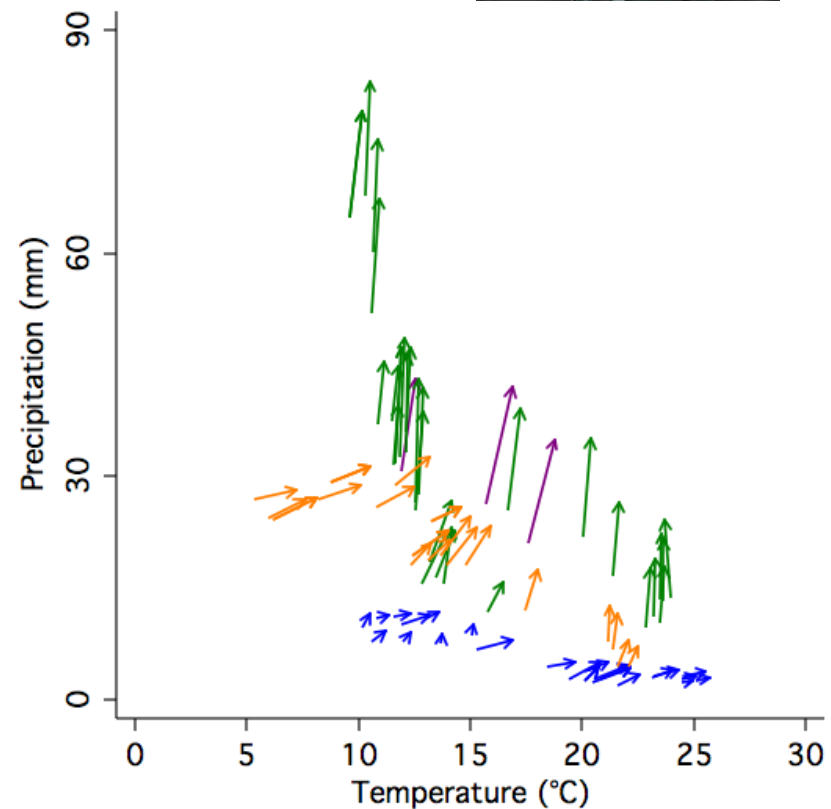
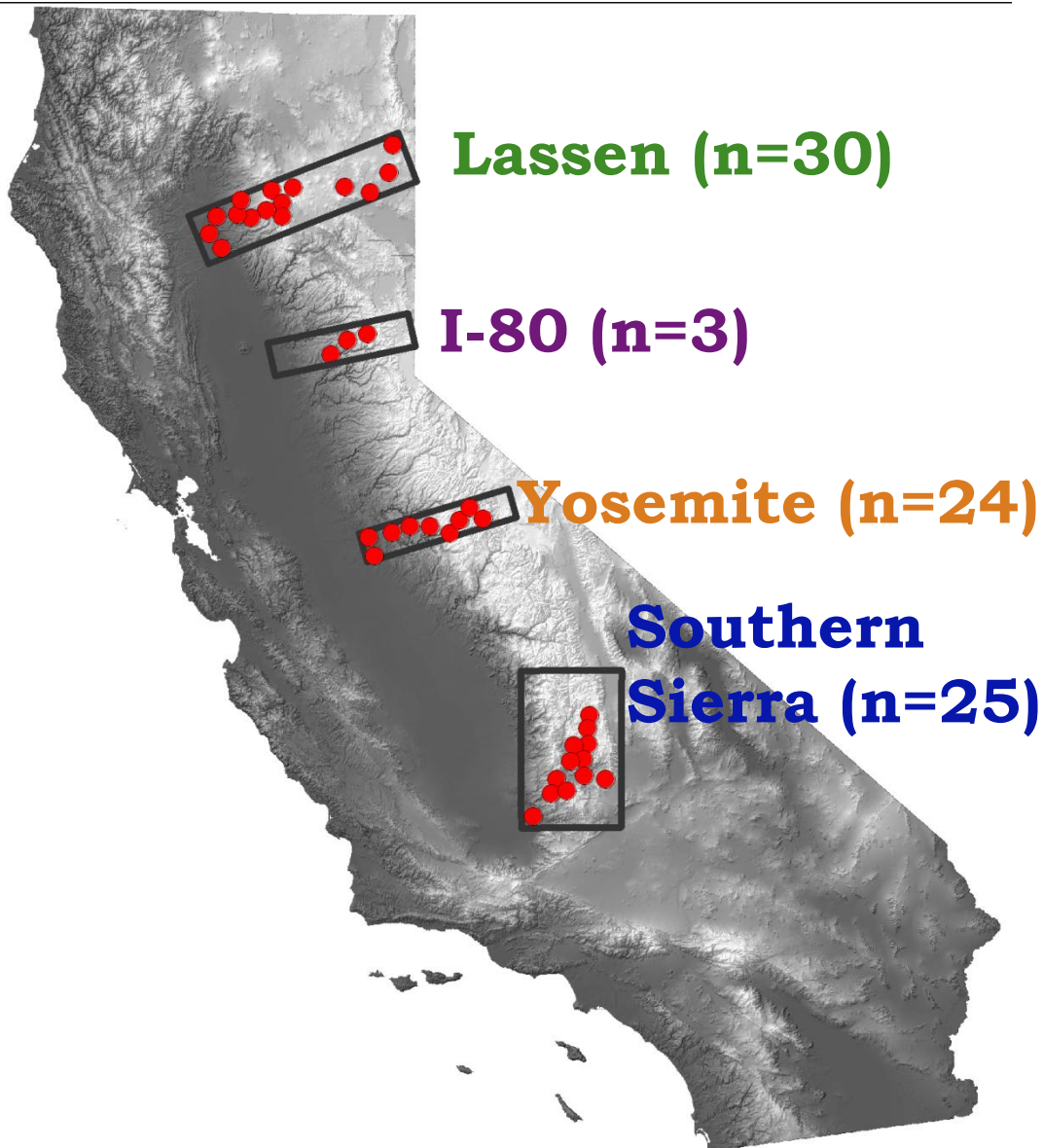
n_{\cdot} - the total number of sites at which the species was detected at least once

n_t - the number of sites where the species was detected at time t .

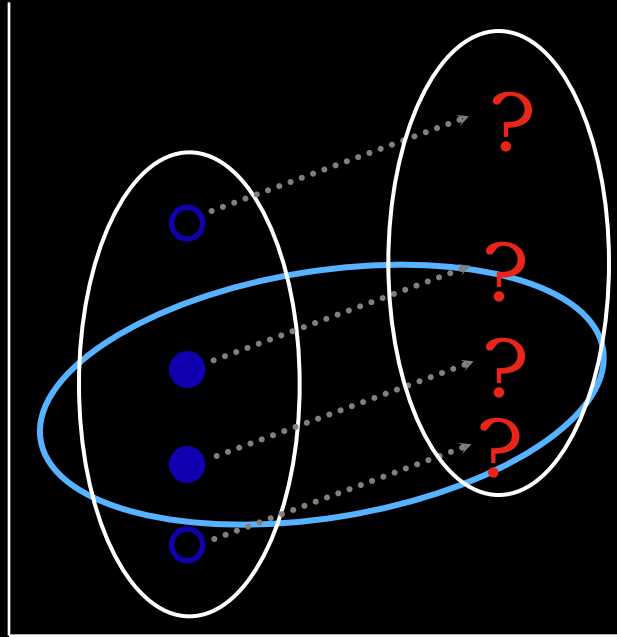
For each small mammal we fit 36 candidate detection models using:

- **Era** (Grinnell vs. Modern)
- **Trend** (declining success by night)
- **Trapping effort** (mean and log number of traps per night)
- And **combinations** and **interactions** (multiplicative and additive) of the above four terms.

Then the 14 best detection models were each used with 8 potential occupancy models to evaluate hypothesized relationships of occupancy with era and elevation.



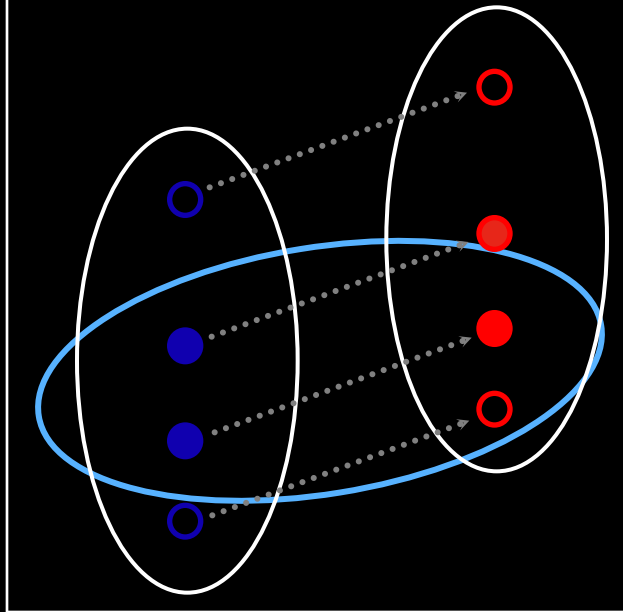
Precipitation



Niche Tracking:
species follow limiting
environmental
boundaries through
geographical space to
remain in favorable
climatic space

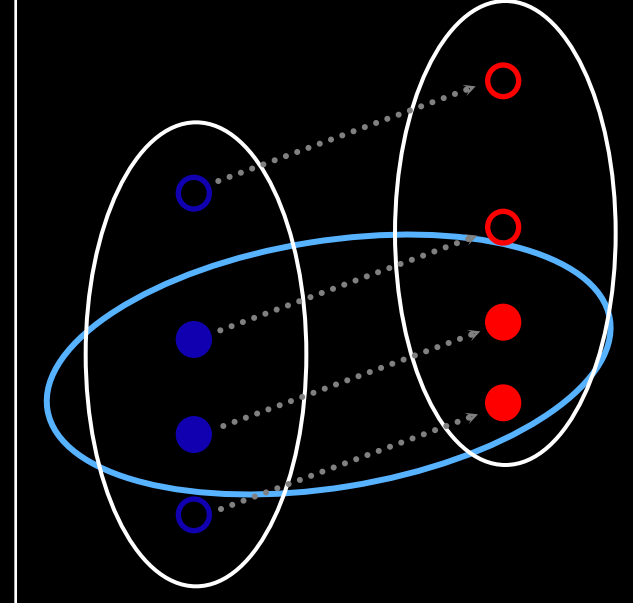
Temperature

Precipitation

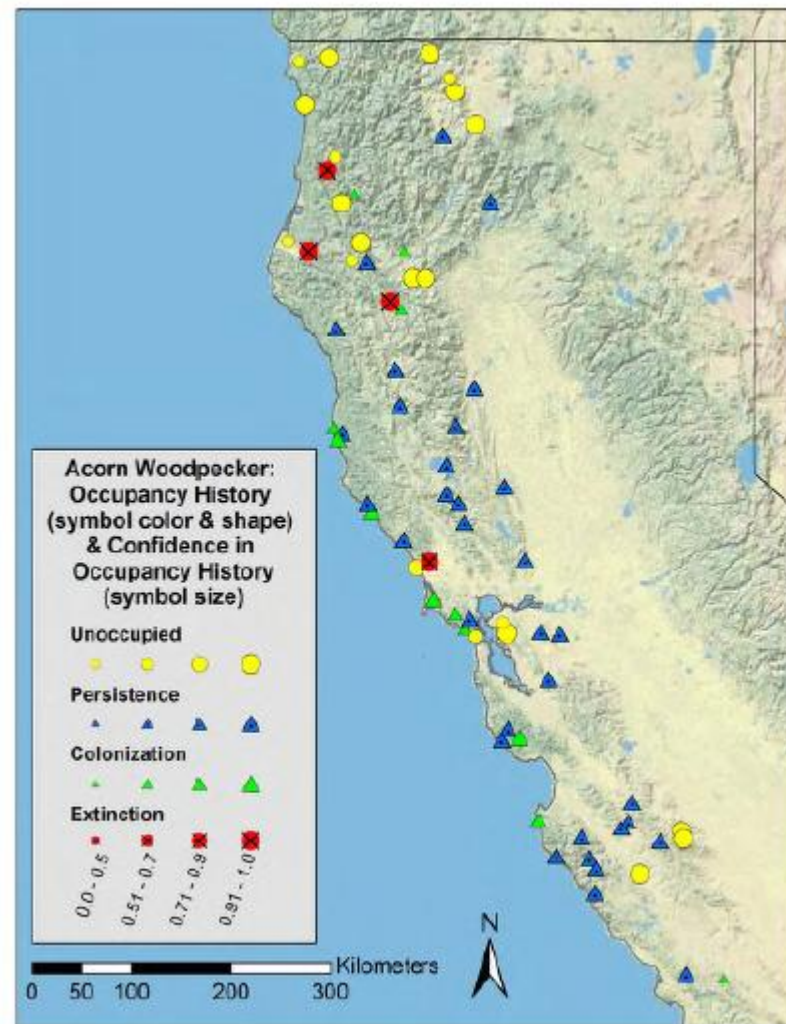
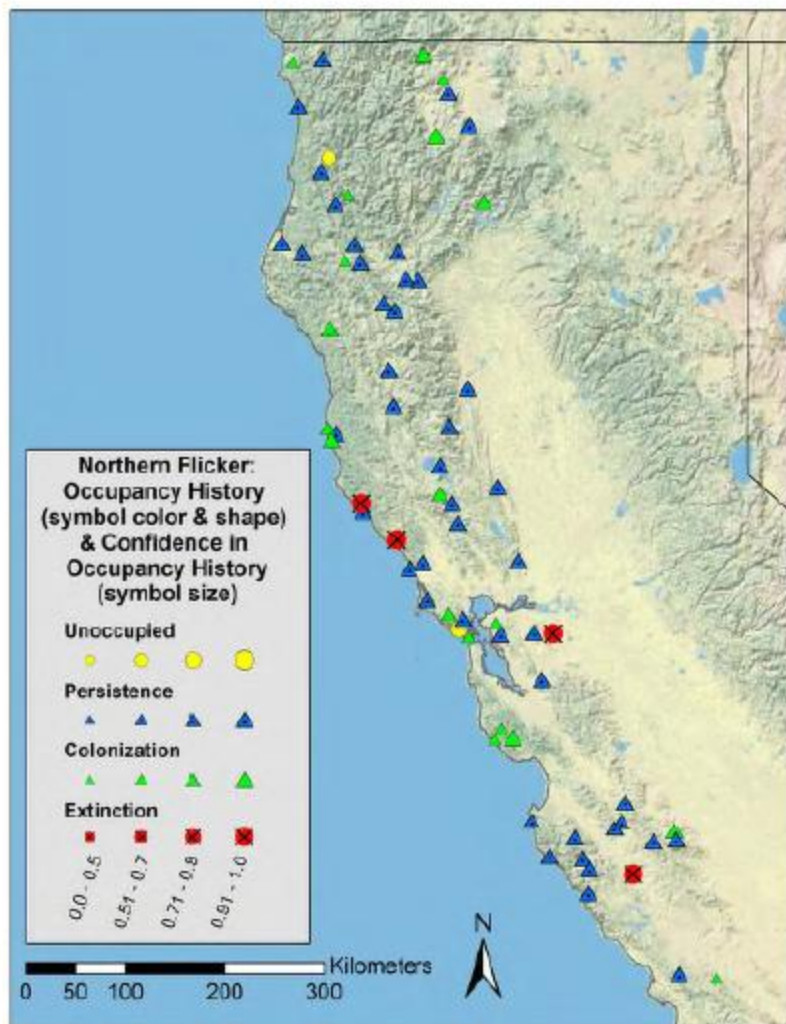


Temperature

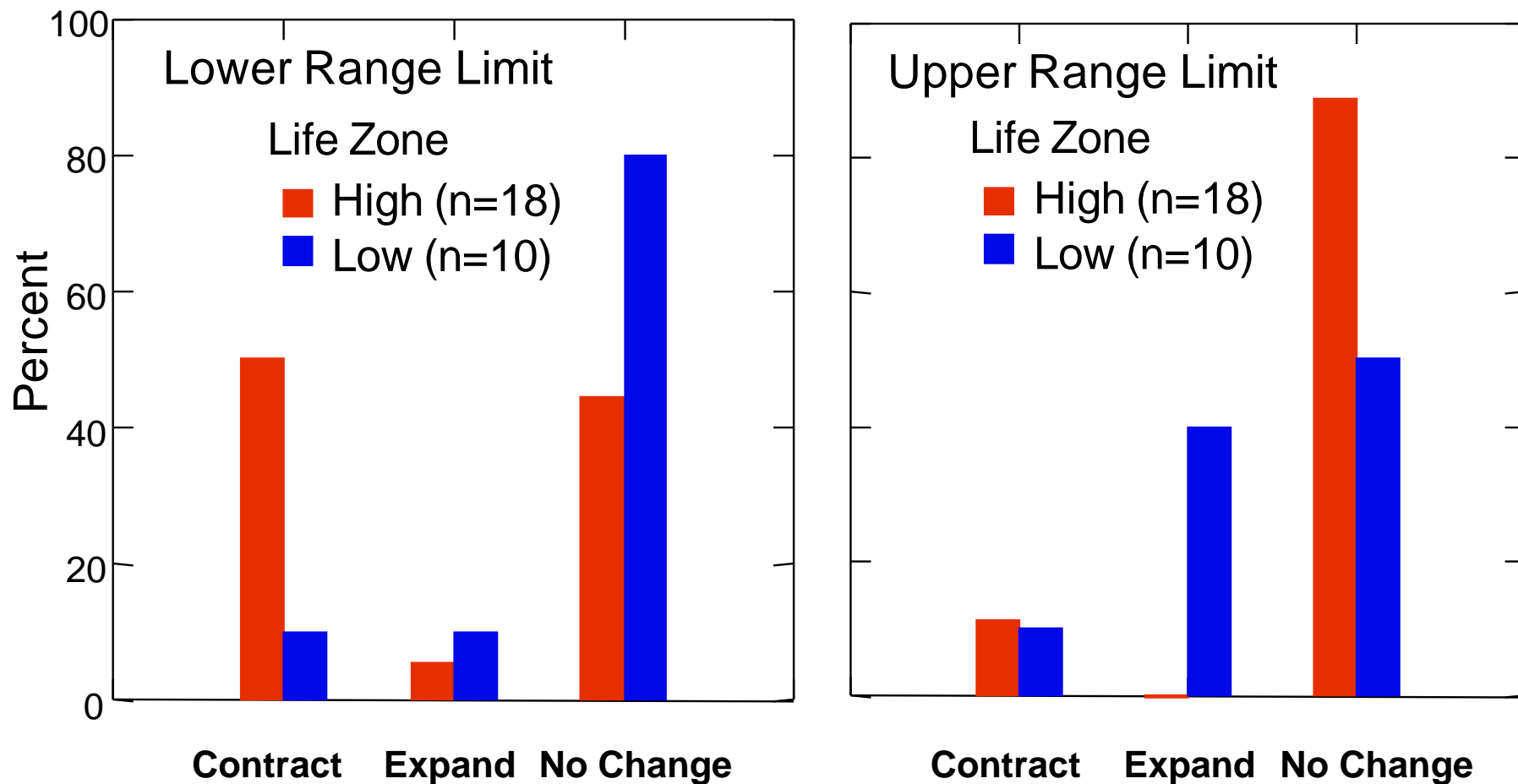
Precipitation



Temperature



High elevation species typically experienced range contractions, whereas low elevation species expanded their ranges upwards ($X^2 = 8.8$, $df = 2$, $P = 0.012$).



Moritz et al. 2008. Science 322: 261-264.

The Grinnellian Niche

“An explanation of this restricted distribution is probably found in the close adjustment of the bird in various physiological and psychological respects to a narrow range of environmental conditions....”

(Joseph Grinnell, *The Auk*, 1917)

